An Anatomical Study of the Genus Echinacea

by Harold W. Keller, Jr.

1962

This thesis was submitted to the Department of Botany and the Faculty of the Graduate School of the University of Kansas in partial fulfillment of the requirements for the degree of Master of Arts.

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Instructor in charge

September, 1962

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For the department

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INTRODUCTION

At the outset, this problem posed interesting taxonomic possibilities as well as contributions to the general field of descriptive anatomy. The purpose of this study is to emphasize both aspects and, where feasible, devise anatomical keys using a combination of characters. The reliability of any key is dependent upon constant characters; therefore, the magnitude of variation in these characters within a species must be taken into account. Any key that is based solely upon individual plant sampling has an inherent weakness. A quantitative statistical treatment of colony samples would be a task beyond the scope of this study. Consequently, the keys constructed herein are practical only within certain limitations but if properly used can be very helpful in determinations.

The genus Echinacea, has important medicinal properties, supplies forage for grazing animals, and is one of many handsome wild flowers that has become such a familiar part of the landscape in Kansas. An ever increasing demand for horticultural varities led to the King, a pink variety, and White Lustre both developed

from Echinacea purpurea. They are desirable as midsummer bloomers adding striking colors and contrast to any garden. The Coneflower or Black Sampson, as it is commonly known, grows abundantly on undisturbed prairies throughout the state of Kansas and acts as an indicator of overgrazing.

This forb was used as a panacea by the Indians. Among some of its reputed virtues were: the root relieved the pain of toothache; the juice soothed burns and aided healing; plants placed in steam baths acted as vaporizers cooling the body from heat discomfort; it was thought to be beneficial in the treatment of mumps and distemper in horses. Pharmaceutical houses even today sell an alcoholic tincture of Echinacea for wounds, skin blemishes, and sore throats.

Echinacea takes its name from the Greek, echinos, meaning hedgehog, and rightly so, as suggested by the spiny pales that form the cone.

Materials and Methods

For the most part, specimens were collected at the University of Kansas Experimental Gardens, Lawrence, Kansas. However, some species were not available necessitating field collections. A complete list of the species and hybrids studied with accompaning field notes is included under collections. All plants studied were collected during anthesis from June 19 to June 22, 1961. Only specific portions of the plant were selected: flower, peduncle, stem, reduced upper leaf, and node with attached leaf.

In order to insure the validity of comparisons organs such as stem and leaf were collected in the same morphological position on each species. This was accomplished by determining a point midway between ground level and flower attachment which served as the source of material for the stem anatomy presented here.

In each case, the first recognizable leaf (not to be confused with reduced upper leaf) borne on the stem below the capitulum was selected for study purposes. This corresponds in some cases to a position just above leaves borne

in somewhat of a rosette-like fashion, especially in the shorter species. Leaf sections were made from stock material cut transversely through the lamina approximately equidistant from base to apex.

Depending on the species, the leaves either have sheathing bases or, as is the case in the narrow-leaf species, tend to be distinctly petiolate. Petiolar anatomy was analyzed from sections taken one quarter inch from the point of departure on the stem axis. Transections of stalked petioles were made halfway between the stem axis and tapering leaf base.

Floral parts such as phyllaries, pales, and ray flowers were sectioned at the approximate midpoint gauged by the overall length of the particular structure. The phyllaries inserted in the outermost position were chosen for sectioning.

After proper selection, the designated materials were placed in vials containing a killing and fixing solution. This fluid, Formalin-Propiono-Alcohol described by Johansen (p. 42), was used exclusively throughout this study.

Two methods of preparation were employed each possessing certain merits. Tissue prepared by the free hand sectioning

method gave excellent preservation of detail, especially in the secretory canal system. However, to produce sections uniform in thickness, less than 10μ, and truly parallel to the plane of cutting requires practice, skill, and patience. Furthermore, sections should be standardized to a certain thickness to study cellular properties on a comparative basis. Vastly superior, then, is the microtome method. But, here again, previous dehydrative treatment entailed before sectioning tends to collapse and distort the thin-walled epithelial cells which surround the canal cavity.

Free hand sections were stained either with safranin and fast green or phloroglucinol in 18% HCl. After passing the stained sections through a graded alcohol series, they were permanently mounted in picolyte. Temporary phloro-glucinol mounts were made by placing sections in glycerin. Moreover, the true nature of the cell (size, shape, and wall thickness) was greatly enhanced when fresh material could be cut, stained and passed directly into glycerin without overuse of a harsh dehydrating agent such as alcohol. This holds especially for collenchymatous tissue which is rich in water and tends to undergo a noticeable

contraction when subjected to dehydrating action. In sections prepared by the paraffin method cortical cells were more compact, thinner walled, and their intercellular spaces completely occluded.

The paraffin method more readily demonstrated the vascularization of the stem axis since whole, intact sections could be obtained. Tissue prepared for the microtome was handled according to the directions given by Johansen (p. 130) whereby tertiary butyl alcohol acts as the dehydration agent. Following impregnation and embedding in paraffin, the material was sectioned with the SPENCER ROTARY MICROTOME at blade settings of 10 and 15 μ. Difficulty in sectioning was encountered where extensive sclerification had occurred throughout the pith region. Even when cut by hand with a safety razor blade the sclerotic material exhibited a tough, woody consistency.

Preleminary staining followed the schedule outlined by Johansen (p. 80-82); however, this was slightly modified to fit each species. An alteration in staining time was made usually with the counterstain, fast green, to get brilliant differentiation.

The presence of a carbohydrate compound, presumably starch, was detected by applying IKI to freshly cut sections. Inulin, reported in the literature as commonly found in roots, sometimes in stems, gives a negative test. Phloroglucinol indicated the extent and relative degree of lignification among the different species.

Macerations.

The stock material was sliced longitudinally into small slivers to increase the disintergrating power and lessen the time required to free the cemented cells. Usually thirty minutes was sufficient time to freely suspend the parenchymatous and collenchymatous cells, but vascular elements often were teased apart with a pin probe. The Macerating fluid was made according to the formula prescribed by Jeffrey, Johansen (p. 104). The range and average measurements of pericyclic fibers, vessels, collenchyma, and parenchyma cells were tabulated from no less than thirty individual cells,

Epidermal Peels.

Thin strips of epidermal cells were peeled from the stem. These were then projected and drawn in surface view

noting the frequency of stomata and trichomes, if any, cuticle characteristics, epidermal patterns, and cell dimensions. Length in surface view refers to cell elongation and orientation in a vertical plane and width to that measurement in a horizontal plane. In transverse stem sections length includes the distance between radial walls and width the distance between tangential walls.

Diagrammatized tissue maps of stem, petiole and leaf midrib transections.

During the course of this study, expediency throughout was made possible with the Bausch & Lomb TRI-SIMPLEX Micro-Projector. It proved indispensable as materials could be projected upon white paper conveniently placed on a table-top, then merely outlining the image. This apparatus was equipped with a tri-objective revolving nosepiece. Their respective magnifications: 2.7 X, 5.0 X, 12.0 X. A special attachment, the 5X Huygenian eyepiece, made possible even greater magnifications. All drawings of stem and petiole transections were made with the 5.0 X objective plus Huygenian eyepiece, a total magnification of 40X.

Leaf midribs were drawn with the 12X objective plus Huygenian eyepiece, a total magnification of 100X.

The different tissue systems are represented thusly: the xylem with associated fibers is lined; the phloem is blank, white; the bundle caps are blackened; and stippling between vascular bundles indicates lignification. The original figures were reproduced by the XEROX photocopying method.

Ray Flowers.

The usage of length and width needs clarification here, since the orientation of adaxial epidermal cells is different than in aforementioned cases. Length refers to the upward, vertical extension of the adaxial epidermal cells exaggerated by their papillose condition. The basal width is in a plane parallel with the surface of the ray flower.

Review of Literature

The Compositae or sunflower family, of which Echinacea is a member, exhibits a wide range of distribution and habit. It is one of the largest of all plant families, including perhaps 20,000 species. This taxon is comprised mostly of herbaceous types, although sometimes shrubby and more rarely woody types occur. Echinacea is herein treated as a herbaceous dicot; however, toward the end of the growing season a small amount of secondary growth may develop not unlike many herbaceous plants. Metcalf and Chalk in their classic two volume work, "Anatomy of the Dicotyledons", list numerous anatomical features which characterize the Compositae. Some of these are: secretory canals, laticiferous canals, glandular and non-glandular hairs, anomalous secondary thickening, medullary bundles, and cortical bundles. Herbaceous stems throughout the family usually exhibit a ring of collateral vascular bundles, each of which is accompanied in the pericyclic region by a large strand of fibers, very often forming distinct "bundle caps."

Even though Echinacea is cited by Solereder (1908), Metcalfe and Chalk (1950), no detailed investigation of

anatomical characters, either on a comparative or taxonomic basis has been published. This intrageneric anatomical treatment will serve, in part, to evaluate taxonomic entities (species, subspecies, varities) based on endomorphic features. The evidence presented here will supplement those exomorphic characters on which identification now is based.

The nature of previous research is arranged categorically to structures. According to Solereder, recognition of families, genera, and even species can be attributed to certain diagnostic anatomical characters. These are included here for the Compositae family. Where special reference is made to Echinacea, as well as many other genera, an asterisk accompanies the character.

Trichomes.

The vestiture usually consists of clothing or glandular hairs. The clothing hairs are generally uniseriate, more rarely biseriate or multiseriate. The simplest uniseriate trichome consists of similar cells except that the terminal cell is pointed or rounded off. The former appears in Echinacea. These trichomes vary in the structure of the basal portion and of the terminal cell.

Crystals.

Calcium oxalate depositions in the form of needles, octahedral, prisms, (rarely in the form of the ordinary larger rhombohedral or clustered crystals) are generally lacking. Inulin is often present particularly in the root and occasionally in the leaf.

Canals.

Schizogenous and lysigenous canals are both common in members of the Compositae, especially in the Tubuliflorae. Generally, resin canals originate by division of the endodermis in the leaf, stem, and more commonly root. Resin canals present in the root usually lack an epithelium; those located in the stem generally have an epithelial lining and are arranged either opposite the vascular bundle or in the interfascicular region. When initiated by the endodermis, the canals mostly lie adjacent to it and on the external side; others however, become situated in the pith or primary cortex of certain species. Structural difference in canal diameter, number, and position were found useful by Van Tieghem (1872). Solereder (1908) states, "the most useful feature for

systematic purposes (mostly as a generic character) is the position of the resin-canals in the stem, whether opposite the vascular bundles or between them." Due to secondary growth some displacement may slightly change the positional arrangement. Canals were recorded Metcalf and Chalk (1958) canals in the cortex, medullary rays and endodermal region extending through the petiole into the leaf in species of Echinacea.* Van Tieghem, Hildebrandt, and Vuillemin reported endodermal resin-canals opposite the vascular bundles in stems of many genera including Echinacea.* As mentioned previously, canals very often occur at the periphery of the pith, usually closely associated with the vascular bundles, either singly or several together. This pattern was found, opposite each vascular bundle in species of Echinacea* by Hildebrandt. The pericycle and primary body generally lack resin-canals except in the aforementioned cases. Many members of the order Tubuliflorae possess secretory organs (oil-canals) particularly in their roots.

Stele.

Hildebrandt's investigations on the varied (parenchymatous or prosenchymatous) differentiation of the interfascicular

tissue and the presence or absence of medullary rays are useful in distinguishing species. The endodermis, sometimes referred to as a "starch sheath", is characterized in some species by Caspary's dots on the radial walls, or by uniformly suberized walls in other species or by the presence of starch in the remainder. Isolated primary bundles of hard bast appear frequently at the inner limits of the pericycle region. Crescent-shaped strands of sclerenchyma cap the vascular bundles adjacent to the phloem, generally originating in the pericycle; less often elements of the phloem proper become sclerosed or lignified. Pith is composed of thick or thin walled cells, sometimes hollow, septate, or sclerified.

Cortex.

The cortex is usually differentiated into an outer collenchymatous portion interspersed with pockets of chlorenchyma, or in other species broad with aqueous tissue, lignified, suberized, or sclerosed.

Epidermis.

The almost universal presence, primarily of the Ranunculaceous (anomocytic) type stomata and less often

the Cruciferous (anisocytic) type, is encountered in the Compositae.

Leaf.

Generally, the dorsiventral type with epidermis not uncommonly including groups of silicified cells is characteristic. A distinct sheath of parenchyma frequently envelops the vascular bundles of veins.

Petiole.

A transverse section at the distal end often will show a simple arc of separate bundles varying from a flattened crescent of a few bundles to a much deeper one consisting of numerous bundles. More complex types include a partly double arch with the adaxial series of bundles inversely orientated. The petiole is often provided with leaf-like wings or with a peripheral zone of chlorencyma. A thick cuticular covering is present along with heavy suberization of ground tissue.

Flowers.

Much attention has been given to floral anatomy. Included under the general heading of floral anatomy are

the comparative aspects of palynology, embryology, histology, fruit histology, floral histology, vascular anatomy, and developmental anatomy. Each subscience has increased our knowledge of phylogenetic trends and, vastly improved on taxonomic criteria.

Noteworthy examples of histological diagnostic characters are (Carlquist, 1957) specific distinction based on the presence and variety of sclerified cells and trichomes at the tips of corolla lobes in Fitchia and (Carlquist, 1959) in Calycadenia; characterization of certain flowers by tanniniferous cells or oil cells (Jonesco, 1932); and kinds of pigmentation described by (Mobius, 1927). Floral nectaries are comparatively discussed by (Fahn, 1955) on morphology, (Feldhofer, 1932) on histology, and (Frei, 1955) on venation.

Apparently the taxonomic importance of peculiar adaxial epidermal cells associated with the petals and marginal rays of many different flowers has been overlooked. General shape and size differences offer excellent characters for specific and even varietal identification within the genus Echinacea.

Description of Stems

E. speciosa. (Fig. 4)

Trichomes and Epidermis

In E. speciosa trichomes are moderately scattered on the stem. These slender, uniseriate hairs average 2.0 mm. in overall length. In basal width, the trichome is (104.0 μ to 135.0 μ), gradually tapering toward the apex. Lengths vary (1.180 mm. to 2.486 mm.) in trichomes, the terminal cell usually being highly variable and often structually modified into a rounded or sharp point. Part way up each trichome, approximately the third cell, sculptured marks appear in the wall. These markings can be aptly described as lenticular. Most of the trichomes have three septations, occasionally four in longer ones. The ontological sequence of the trichome conforms to the generic pattern in which only epidermal cells undergo division (Fig. 42). However, the trichome is raised on a supporting base formed from both epidermal and sub-epidermal cells. In surface view they appear morphologically distinct from the surrounding epidermal cells.

Epidermal cells in surface view have a highly irregular outline, accounting for the wide range in size (Fig. 39). This, no doubt, is due to the fluted surface of the stem which tends to give smaller, more rectangular shaped cells in the grooves, and larger, more angulate cells on the ridges. Lengths range from 183.0 μ to 156.0 μ and average 104.0 μ. Widths range from 24.2 μ to 52.0 μ and average 38.0 μ. In transverse section the cross diameter ofepidermal cells is uniform, unlike the length, which varies considerably. The stomata are of the anomocytic type (lacking subsidiary cells).

Cortex.

Small pockets of thin-walled chlorenchymatous cells underlie each substomatal chamber. These fan out short distances around the stem and are interrupted at intervals by collenchyma which directly abuts the epidermis. Generally three types of collenchyma are recognized: angular, lamellar, and tubular. All three types often intergrade; however, the tubular type, with intercellular spaces and angular thickenings, is predominant

in Echinacea. Their general shape consists of elongate cells having unevenly thickened walls, with either rectangular, oblique, or tapering ends. A transitional region between cortical collenchyma and parenchyma occurs within one of two rows outside of the endodermis. Size and shapes of collenchyma cells were studied from longitudinal sections and macerations. Length ranges from 124.0 μ to 280.0 μ with numerous cells in the 156.0 μ to 208.0 μ range. Width ranges from 27.0 to 41.0, 28.0 μ being common. Fibers and sclereids are absent. A measurement including endodermis, cortex, and epidermis ranges from 156.0 μ to 312.0 μ, generally falling between 208.0 μ and 260.0 μ.

Endodermis.

In transverse section, the uniseriate endodermis is recognizable by the elliptic, thin-walled cells lacking pits. A starch test with IKI gave a positive reaction (a dark blue-black color) confined mostly to the endodermal layer. Instead of giving a blue ring, groups of two or three cells were filled with starch grains; then, for some distance, there occurred cells void of starch. The

starch granules, which measure 43 μ in. cross diameter, appear roundish, and the surface rough.

Pericyclic Fibers.

Before correct nomenclatorial assignment of fibers can be made, a study of development and differention must be determined. Regardless of phloic or pericyclic origin, pericyclic fibers refer here to those of the "bundle caps." In transection, the radial extent ranges from 83.0 to 135.0 μ. As seen in maceration the longest fibers, 1,341.0 μ, and the shortest, 322.0 μ , vary in shape; some are tapered to a sharp point, others blunt, and still others, truncate. All fibers have reduced slit-like pits. They average in length 761.0 μ and in width 16.0 μ. The width ranges from 31.0 μ to 9.7 μ . Fibers give a strong positive phloroglucinol reaction. Lumen diameter ranges from 24.2 μ to 4.0 and averages 11.3 μ .

The phloem zone measures 50.5 μ to 75.0 μ in radial extent. No crystals or storage products are present.

In transection the number of rows of metaxylem vessels range from three to seven. Interspersed between the metaxylem vessels are fibers. As seen in macerations, vessel lengths vary from 644.0 to 197.0 μ and average 419.8 μ. The end walls are completely dissolved out, resulting in the simple perforation type. Shapes vary some are barrel shaped with horizontal end walls, others oblique and pointed. No annular vessels were observed and tracheids were absent. Vessel widths range from 24.2 μ to 41.6 μ . Vessels with spirals (all degrees loose to close spirals) range from 364.0 μ to 1,008.0 u . Protoxyem points number 31. Radial extent of vascular bundle ranges from 500.0 μ to 240.0 μ . Pitted vessels range from sclariform to elliptic.

Pith.

Pith diameter is 3.3 mm. Intercellular spaces in the pith measure 1.0 μ . Lengths of individual cells range from 104.0 μ to 177.0 μ and average 135.0 μ The widths range from 52.0 μ to 104 μ and average 83.0 μ Pith cells are densely pitted. Cells are nearly iso-

diametric, loosely arranged, and have no regular arrangement of cells. Cells in the center are larger, merging toward the periphery into smaller, thicker walled cells. These cells, however, fail to form a definite enough zone to be called perimedullary. Those cells supporting bundles tend to become scleritized. Also, scleritized cells surround the resin canals. No sclerotic cells are present in the center of the pith.

Secretory System.

Canals in this species originate adjacent to, and through the division of the endodermis. Formation within the interfascicular region remains the rule, the exception being in those cases where surrounding cells of the vascular system undergo positional rearrangement, tending to relocate the canal along the ascending arc of the bundle caps. Canals also are found either singly or in pairs closely associated with the vascular bundle at the periphery of the pith. (Fig. 60) These appear to be an integral part of the vascular bundle, but they actually form outside of an opposite the protoxylem points, becoming surrounded by cells that are highly lignified.

Pith canals number 36 as seen in cross section. The diameter of pith canals ranges from 24.0 μ to 50.0 μ and averages 38.0 μ. Such a great range can be attributed to the developmental stage of the canal. Smaller canals have reduced cavities and large, relatively few epithelial cells. The larger ones have an enlarged cavity and smaller, relatively many epithelaial cells. As mentioned previously, the epithelial cells vary markedly in size and even in shape. They range from 16.9 to 21.8 μ between anticlinal walls. The number of epithelial cells lining the cavity varies from four to seven. Epithelial cell shape varies from square to oblong rectangular; some areovoid but always the walls form an oblique angle. Each epithelial cell has a dense cytoplasmic content with a conspicuous nucleus. When present in pairs they appear in a juxtaposition sometimes spatially separated by as much as 100.0 μ. Cortical canals tend to be crushed in sectional view. In addition, the epithelial cells are often not well differentiated from the surrounding cortical parenchyma. From 20 to

24 canals are present in the cortical region. Cortical canals are usually spherical in shape and range from 41.0 μ to 48.0 μ and average 45.0 μ . in cross diameter.

General Remarks.

The stem diameter is relatively large. Because there is enough sclerification of the interfascicular region, medullary rays do not unite the cortex. The stelar configuration seems to follow a circular design. Only in a portion of the stem does secondary growth begin.

E. leavigata (Fig. 1)

Trichomes and Epidermis

Trichomes are absent. Epidermal cells in surface view range from 82.0 μ to 190.0 μ and average 150.0 μ in length. Widths range from 32.0 μ to 50.0 μ and average 38.0 μ . In every dimension, the epidermal cells are larger than in other species. Moreover, a striking pattern of straight, oblique, and curved walls demonstrates the irregularity in cell shape. (Fig. 36)

Cortex

Only the outermost layers consist of typical collenchyma. The greater part of the cortex is parenchymatous tissue with large intercellular spaces (10.0 μ). The breadth of the cortex extends from 325.0 μ to 700 μ. In longitudinal section collenchyma cells range from 74.0 μ to 136 .0 μ and average 110.0 μ. Widths range from 60.0 μ to 78.0 μ and average 65.0 μ.

Pericyclic Fibers

This species gives a weak phloroglucinol test. The fibers, mostly thin and needle like in structure,

are easily broken into fragments. The end walls taper to a very sharp point. Lengths vary from 360.0 to 1150. μ and average 794.0 μ. Widths range from 8.0 μ to 20.0 μ and average 13.0 μ.

Xylem and Phloem

The phloem zone is 60.0 μ to 70.0 μ in radial extent. Vessels, as seen in maceration, range in length from 159.0 μ to 450.0 μ and average 302.0 μ. Their widths range from 23.0 μ to 34.0 μ and average 29.0 μ. Some of the scalariform vessels are tailed with oblique perforation plates. Other features are: 44 protoxylem points, a vascular bundle breadth of 400.0 μ to 575.0 μ, and very little sclerification between vascular bundles.

Pith

No sclerids are present. Lengths range from 60.0 μ to 174.0 μ and average 121.0 μ. Widths range from 60.0 μ to 97.0 μ and average 80.0 μ. The diameter of the pith is 4.2 mm.

Secretory System

Canals are present in the cortex and pith. Those of the cortex are relatively large with usually five

to eight epithelial cells. Canals range from 40.0 μ to 57.0 μ and average 50.0 μ. Canals located in the cortex are relatively abundant (48±2), originating opposite the vascular bundles and/or interfascicular region. In the pith, canals form double rings of epithelial cells as a result of a second periclinal division. Consequently the outer ring has elliptic cells, the inner one rectangular. About half of the vascular bundles have single canals; the others occur in pairs. Canals are either centric or excentric depending on whether they occur opposite the protoxylem points or along side the vascular bundle. Here, one canal is usually centric, and one or two, whichever the case may be, excentric. Pith canals range from 34.0 μ to 50.0 μ and average 45.0 in cross diameter. Generally, five to eight epithelial cells surround the canal cavity. Canals of the pith total 58±2, a relatively large number.

General Remarks:

Medullary rays extend into the cortex with only partial sclerification. These rays can be called parenchymatous.

E. purpurea (Fig. 2)

Trichomes and Epidermis

Trichomes thickly cover the stem. The base of the trichome is swollen and accentuated by an outgrowth of surrounding epidermal cells. Repeated sectioning was required to get thin paradermal peels. Heavy pubesence undoubtedly caused this difficulty. In surface view the margin of the cuticle is wavy and rough in outline. Striae or rod-like bodies decorating the surface of the epidermis were ascribed to cuticle depositions. Again, as in other species, the stem is grooved. In surface view, epidermal cells vary in length from 82.0 μ to 142.0 μ and average 115.0 μ. Widths of these cells range from 25.0 μ to 37.0 μ and average 30.0μ. Epidermal cells have some rectangular end walls which are usually oblique and angulate. (Fig. 37)

Cortex

The cortex contains an outer, several layered, narrow zone of collenchyma and an inner, many layered, loosely arranged, broad zone of parenchymatous tissue. Collenchyma cell lengths range from 111.0 μ to 157.0 μ and average 131.0 μ. Widths range from 21.0 μ to 37.0 μ and average 30.0 μ.

Pericyclic Fibers

A moderate phloroglucinol test is shown by the bundle caps. Fibers range in length from 663.0 μ to 2,400.0 μ and average 1,288.0 μ. Widths range from 8.0 μ to 22.0 μ and average 15.0 μ. The average wall thickness is 5.0 μ and lumen size is 7.0 μ.

Xylem and Phloem

The phloem zone radially extends from 59.0 μ to 73.0 μ. Vessel lengths range from 232.0 μ to 680.0 μ and average 460.0 μ. Widths range from 20.0 μ to 42.0 μ and average 32.7 μ. Other features include: five to eight metaxylem rows (five being most common), 42 protoxylem points, and a vascular bundle breadth of 250.0 μ to 550.0 μ.

Pith

The diameter of the pith is 3.6 mm. No sclerids are present. Lengths range from 92.0 μ to 130.0 μ and average 123.0 μ. Widths range from 93.0 μ to 110.0 μ and average 100.0 μ.

Secretory System

Canals occur in both the pith and cortex. Those of the cortex tend to be tangentially flattened and are located opposite both vascular bundle caps and interfascicular regions. Epithelial cells are in direct contact with the endodermis and are not well differentiated from surrounding parenchymatous tissue. Epithelial rings of five to eight cells surround canals which range from 41.0 μ to 55.0 μ and average 51.0 μ. Cortical canals number more than 48. Pith canals tend to be less numerous (34±2) and centric or excentric in position. A range from 34.0 μ to 51.0 μ averaging 41.0 μ is found in the pith canals. They have epithelial cells with elliptic to subspherical shapes. No tangential divisions were observed in epithelial cells.

General Remarks

The vascular stele is broken up into a dictyostele. Medullary rays pass out into the cortical tissue.

E. pallida (Fig. 3)

Trichomes and Epidermis

Trichomes are moderately scattered over the stem surface. Three to five septations divide each trichome into four or five cells at irregular intervals. Generally the trichome is slender and tapered to a sharp point. Lengths range from one to two mm. In surface view the epidermis has angulate and rectangular cells; this is expressed in transection notably in the irregularity of epidermal cell size and shape. Paradermal sections were difficult to make due to the grooves and thick cuticle. The cuticuler layer was 7.0 μ thick, bearing tiny spine-like projections on the surface. The inner tangential wall is heavily cutinized. In surface view widths of epidermal cells range from 28.0 μ to 53.0 μ and average 41.0 μ. In length these cells range from 65.0 μ to 150.0 μ and average 113.0 μ. (Fig. 41)

Cortex

The cortical zone (including endodermis and epidermis) measures 180.0 μ at the narrowest point and 430.0 μ at the broadest. Collenchymatous tissue makes up most of the cortex. As seen in maceration, collenchymatous cells

range in length from 110.0 μ to 280.0 μ and average 189.0 μ. In width these cells measure 36.0 to 46.0 μ and average 45.0 μ.

Pericyclic Fibers

Fibers, as seen in maceration, range from 450.0 μ to 1,450.0 μ and average 1,056.0 μ. Widths range from 40.0 μ to 18.0 μ and average 27.0 μ. Lumen diameter is 8.0 μ to 16.0 μ.

Xylem and Phloem

The phloem zone measures 60.0 μ to 90.0 μ in radial extent. Xylem elements consist of vessels, fibers, and xylem parenchyma. Macerations of vessel elements range in length from 215.0 μ to 610.0 μ and average 378.0 μ. Widths range from 40.0 μ to 51.0 μ and average 48.0 μ. No annular vessels or tracheids are present. All vessels have simple perforation plates. The protoxylem, mainly spiral vessels, and the metaxylem, with sclariform to definite reticulate pits, seem to be developmentally more advanced than in E. speciosa. A weak phloroglucinol test was obtained in this species. Other vascular features are: three to nine rows of metaxylem, vascular bundle breadth of 500.0 μ to 750. μ, and 34 protoxylem points.

Pith

Pith diameter is 3.2 mm. No sclerids are present. The pith consists wholly of parenchymatous tissue. Length ranges from 74.0 μ to 135.0 μ and average 101.0 μ. Widths range from 72.0 μ to 110.0 μ and average 105.0 μ.

Secretory System

Secretory canals are present in both cortex and pith. Undeveloped canals have approximately four epithelial cells and a small canal cavity. These arise through radial (anticlinal) divisions sometimes followed by a tangential division that gives a rectangular shape to the epithelial cells. With the completion of these divisions, the epithelial ring consists of at least six cells with an enlarged cavity. Canals of the pith appear singly, in pairs, and in triplets opposite the protoxylem points; when farther removed, the intervening cells become strongly sclerified. To ascertain an arrangement of pith canals is difficult. The significance of the overunder, juxtoposed or fused arrangement is open to argument. From three to seven epithelial cells delimit the pith canals. They range from 32.0 μ

to 45.0 μ and average 40.0 μ. Often thin-walled accessory tissue occurs above or surrounds some canals, but not all. More rarely, it replaces the canal appearing in the same morphological position. Not all of the pith canals are well-defined. Small patches of thin-walled cells (11-15) are designated accessory tissue. This tissue stains green with fast green stain. The pith canals in this species tend to anastomose, still, however, maintaining their individual identity. Cortical canals are spherical in shape ranging from 35.0 to 46.0 μ. Each bundle cap has one canal on each side lying adjacent to the endodermis in the interfascicular region.

General Remarks

Only in this species are the collateral vascular bundles united in a ring (siphonostele) through initiation of the interfascicular region. The author wishes to point out that an error in the diagram (Fig. 3) fails to show secondary growth in some cases. Stippling can represent this secondary growth. Vascularization in this species makes up the greatest fraction of the stem. The stele has a columnar configuration tending to be pentagonal.

E. sanguinea (Fig. 11,65)

Trichomes and Epidermis

Trichomes thickly cover the stem. A short, stout trichome, usually with fewer septations, typifies this species. (Fig. 44,45) The base of the trichome is heavily cutinized. In surface view, lengths of epidermal cells range from 60.0 μ to 170.0 μ and average 120.0 μ. Widths range from 31.0 to 46.0 μ and average 42.0 μ. Epidermal pattern consists of straight, mostly rectangular cells. (Fig. 35)

Cortex

Collenchymatous tissue makes up the greater part of the cortex, excepting several parenchymatous layers outside of the endodermis. Lengths in these elongated, tapered cells range from 151.0 μ to 373.0 μ and average 180.0 μ. Widths range from 40.0 μ to 45.0 μ and average 43.0 μ. Cortical breadth ranges from 190.0 μ to 230.0 μ.

Pericyclic Fibers

Fibers of this species tend to be thicker with blunt or truncate ends. They are not fragile or needle-like. Lengths range from 300.0 μ to 1,350.0 μ and average 850.0 μ. Widths range from 17.0 μ to 21.0 μ.

Xylem and Phloem

The phloem zone in radial extent is 22.0 μ to 45.0 μ. Vessel lengths range from 275.0 μ to 950.0 μ and average 523.0 μ. These cells in width range from 20.0 μ to 35.0 μ and average 29.0 μ. Other features consist of: 18 protoxylem points, three to five metaxylem rows (usually three), and little or no sclerification between vascular bundles.

Pith

No sclerids are present in the pith. These cells range from 89.0 μ to 176.0 μ in length and average 137.0 μ. Widths range from 41.0 μ to 105.0 μ and average 72.0 μ. Pith diameter is 1.4 mm., the smallest of all species studied. The walls of the parenchyma cells are densely marked with primary pit fields. These pits are elliptic and very conspicuous.

Secretory System

These canals are truly interfascicular in origin. A brownish substance appears in some of the epithelial cells, making their presence conspicuous; others, however,

were colorless and less conspicuous. Canals range from 40.0 μ to 48.0 μ with either a five or six-celled epithelial ring. An average of 42.0 μ for canals was recorded; moreover, between 13 and 15 canals occur in the cortex.

General Remarks

The lack of a secretory system and sclerotic cells in the pith makes relationship problematical. The relatively small amount of vascularization reflects the spindley habit of the plant. Furthermore, medullary rays tend to be prosenchymatous and sclerified, previously mentioned as a distinguishing character for any species.

E. atrorubens (Fig. 5, 66)

Trichomes and Epidermis

Trichomes are sparsely present. Often they are wanting on portions of the stem. In surface view, lengths of epidermal cells range from 42.0 μ to 100.0 μ and average 77.0 μ. Widths range from 24.0 μ to 42.0 μ and average 38.0 μ. Paradermal sections can be peeled easily unlike many other species. Generally the epidermal pattern consists of rectangular, nearly isodiamentric cells, with mostly straight end walls. Occasionally the walls do slant so that areas may be irregular.

Cortex

Cortical breadth is uniform throughout the stem ranging from 350.0 μ to 400.0 μ. Cortical tissue consists of an outer collenchyma zone and inner parenchymatous region.

Xylem and Phloem

Phloem zone ranges from 42.0 μ to 56.0 μ in radial extent. Other features include: three or four metaxylem rows, 38 protoxylem points, and vascular bundle breadth 300.0 μ to 550.0 μ.

Pith

No sclerids are found in the pith. The pith diameter is 3.0 mm. Lengths of pith cells range from 40.0 μ to 92.0 μ and average 68.0 μ. Widths range from 41.0 μ to 110.0 μ and average 78.0 μ.

Secretory System

Canals are present in both pith and cortex. Pith canals range from 45.0 μ to 60.0 μ and average 54.0 μ in cross diameter. Moreover, an area of thin-walled accessory tissue is arranged above canals, surrounding canals, and not infrequently in the same morphological position of the canals. (Fig. 61,62) Epithelial rings contain four to eight rectangular or diamond shaped cells. Tangential divisions occur halfway around the canal to give a partial double ring The cavity of these canals ranges from 20.0 μ to 30.0 μ, so are very conspicuous. Usually a single well-defined canal is located opposite the protoxylem points. Only 20 canals were counted in the pith. Cortical canals range from 40.0 μ to 52.0 μ and average 46.0 μ in cross diameter. These canals originate opposite the inter-fascicular region.

General Remarks

This species gives the strongest phloroglucinol test. For the most part vascular bundles are discrete separated by slightly sclerified tissue. The interfascicular region has prosenchymatous tissue.

E. paradoxa var. paradoxa (Fig. 6)

Trichomes and Epidermis

Only two trichomes occur on the stem segment selected for study. Trichomes, then, are greatly reduced in numbers. The stem lacks grooves at this position so that paradermal sections show uniformity in cell shape. Of special interest is the constant rectangular shape of epidermal cells in surface view. (Fig. 30,31) In transectional view many cells are squarish instead of the typical tabloid epidermal cell. Cuticle seems to consist of double layers 10.0 μ thick. Anticlinal walls of epidermal cells are thin and straight. In transection length averages 22.0 μ and width 18.0 μ. In surface view epidermal cells range in length from 40.0 μ to 110.0 μ and average 90.0 μ. These cells range in width from 26.0 μ to 34.0 μ and average 30.0 μ.

The cortex is made up of an outer collenchyma zone and an inner parenchymatous tissue with large intercellular spaces. Lengths of collenchyma cells range from 90.0 μ to 228.0 μ and average 180.0 μ. Widths range from 28.0 μ to 61.0 μ and range 45.0 μ.

Pericyclic Fibers

Lengths of fibers range from 475.0 μ to 2,200.0 μ and average 1,190.0 μ. Widths range from 16.0 μ to 25.0 μ and average 20.0 μ. The average wall thickness of fibers is 6.0 μ in this species. The lumen ranges from 6.0 μ to 10.0 μ.

Xylem and Phloem

The phloem zone measure 50.0 μ to 95.0 μ in radial extent. Vessels range in length from 325.0 μ to 650.0 u and average 485.1 μ. Widths range from 23.0 μ to 50.0 u and average 33.0 μ. Other features of the xylem include: four to eight metaxylem rows, (five commonly) 32 protoxylem points, and vascular bundles breadth 300.0 to 600.0 μ.

Pith

The diameter of the pith is 3.0 μ. Lengths of pith cells range from 83.0 μ to 215.0 μ and average. No sclerids are present in the pith.

Secretory System

Canals are present in both pith and cortex. Many of the pith canals are comparatively small; however, some

canals range up to 65.0 μ in cross diameter. These canals range from 30.0 μ to 65.0 μ and average 50.0 μ. Generally canals occur singly opposite protoxylem points. Epithelial rings consist of four to six cells positioned to give a hourglass or star-shaped canal cavity. Canal cavities are reduced in size. As a general rule canals lie adjacent to the endodermis layer. Cortical canals originate opposite vascular bundle caps and interfascicular regions. These canals range from 40.0 μ to 65.0 μ and average 60.0 μ. Epithelial rings consist of five to eight cells.

General Remarks

Secondary growth occurs on one side of the stem but apparently is lacking on the other. One would expect a more uniform activity of the cambium.

E. paradoxa var. neglecta (Fig. 7)

Trichomes and Epidermis

Trichomes are very few or wanting. This species has one of the most distinctive epidermal patterns. (Fig. 27, 28,29) In surface view epidermal cells are uniform in shape and significantly smaller in width. Overall cell dimensions are relatively small. Lengths of epidermal cells range from 41.0 μ to 107.0 μ and average 80.0 μ. Widths of these cells range from 27.0 μ to 37.0 μ and average 33.0 μ.

Cortex

The breadth of cortical tissue extends from 230.0 μ to 500.0 μ. An outer portion of the cortex is chiefly collenchyma while the inner portion intergrades into parenchymatous tissue.

Xylem and Phloem

Phloem zone extends from 46.0 μ to 56.0 μ. Xylem features include: three to five metaxylem rows, 42 protoxylem points, and vascular bundle breadth 450.0 μ to 250.0 μ.

Pith

Cells of the pith are strikingly uniform in this species. Lengths of these cells range from 137.0 μ to 257.0 μ and average 189.0 μ. Widths range from 33.0 μ to 65.0 μ and average 47.0 μ. Pith diameter is 2.85 mm. No sclerids occur in the pith. In longisection densely pitted cells can be seen.

Secretory System

Canals are present in both cortex and pith. Those of the pith range from 30.0 μ to 70.0 μ and average 55.0 μ. Many canals are tangentially flattened especially larger ones. Canals occur either in ones, twos, or threes, opposite protoxylem points. (Fig. 57) Canals that occur along side the vascular bundle are never more than 45.0 μ; while those opposite protoxylem points are relatively large 50.0 μ to 70.0 μ. Epithelial rings consist of 5 to 15 cells rectangular in shape. (Fig. 58,59) Accordingly, the canal cavity is relatively large from 20.0 μ to 36.0 μ. Some canals are very near protoxylem points; others, however, may be removed as much as 100.0 μ. Cortical canals range from 45.0 μ to 75.0 μ and average 60.0 μ. Interestingly,

many canals are found removed some distance from their site of origin, the endodermis. Epithelial rings consist of 8 to 14 cells. Canals originate opposite both the vascular bundle caps and interfascicular regions. The newly formed canals are much smaller and confined to the endodermal layer; while those embedded in cortical tissue are well-defined and relatively large.

General Remarks

This species has no secondary growth although interfascicular regions are highly sclerified. In addition to the prominent secretory system, the width of pith cells is significantly less. Vascular bundles on one side of the stem tend to be much smaller than on the other side.

E. angustifolia var. angustifolia race intermedia (Fig. 8)

Trichomes and Epidermis

The stem is heavily covered with trichomes. They are shorter, 0.5 mm. to 1.5 mm., and stouter than in other species. Either two or three septa occur with conspicuous lenticular bumps in the trichome wall. A thick (9.0 μ) cuticle covers the outer tangential wall and cutinzation is evident in the inner tangential wall. Prominent short, spin-like projections mark the surface of the cuticle. In surface view, epidermal cells in length range from 61.0 μ to 122.0 μ and average 103.0 μ. Widths of these cells range from 26.5 μ to 36.0 μ and average 33.0 μ. In surface view rectangular and oblique walled epidermal cells can be seen. (Fig. 38)

Cortex

Cortical breadth ranges from 350.0 μ to 750.0 μ. The cortex is largely made up of collenchyma that ranges in length from 120.0 μ to 300.0 μ and averages 228.0 μ. Widths of these cells range from 44.0 μ to 56.0 μ and average 45.0 μ.

Pericyclic Fibers

Lengths of fibers range from 560.0 μ to 1,700.0 μ and average 896.0 μ. Widths of these cells range from 13.0 μ. The wall thickness of fibers average 5.0 μ. Some fibers have rough, wavy walls with extremely long, sharp points; others, are blunt or gradually tapered.

Xylem and Phloem

The radial edtent of phloem is 58.0 μ to 73.0 μ. Lengths of vessels range from 230.0 μ to 700.0 μ and average 446.0 μ. Widths of vessels range from 25.0 μ to 38.0 μ and average 33.0 μ. Many vessels are tailed with oblique perforations. Other xylem features include: three to four metaxylem rows, 24 protoxylem points, and vascular bundle breadth 450.0 μ to 550.0 μ. The vascular bundles are surrounded by a relatively large amount of fibrous tissue.

Pith

Pith diameter is 1.3 mm. Sclerotic cells occur throughout the pith. Lengths of these cells range from 72.0 μ to 232.0 μ and average 141.0 μ. Widths range from 24.0 μ to 67.0 μ and average 48.0 μ. Elliptic pits densely occur in

the walls. In longisection dark streaks between adjacent sclerotic cells is a result of the black substance occluding intercellular spaces. (Fig. 67)

Secretory System

Canals are absent in the pith. Those of the cortex appear opposite the vascular bundle caps and interfascicular region. Canals range from 33.0 μ to 48.0 μ and average 40.0 μ in cross diameter. From five to seven celled epithelial rings surround the small canal cavity. A total of 26±2 canals was recorded in the cortex.

General Remarks

No medullary rays are present due to extensive amounts of fibrous tissue. In fact, several vascular bundles seem to have undergone fusion undoubtedly caused by this fibrous tissue.

E. angustifolia var. strigosa (Fig. 9)

Trichomes and Epidermis

Trichomes thickly cover the stem. In surface view epidermal cells in length range from 27.0 μ to 57.0 μ and average 49.0 μ. Widths range from 27.0 to 40.0 μ and average 33.0 μ. The epidermal pattern consists of relatively small rectangular cells. (Fig. 33)

Xylem and Phloem

Features of the xylem include: 24 protoxylem points, two to five metaxylem rows, and vascular bundles breadth 250.0 μ to 400.0 μ.

Pith

Sclerids occur throughout the pith. Unsclerified cells range in width from 38.0 μ to 88.0 μ and average 65.0 μ. Sclerified cells range in width from 30.0 μ to 52.0 μ and average 45.0 μ. Pith diameter is 1.6 mm. The pith becomes sclerified at a lower level in the plant body than in other species.

Secretory System

Canals are present only in the cortex. These canals range from 38.0 μ to 55.0 μ and average 43.0 μ. A total number of 26 canals occur in transectional view. One anomolous canal formed inside a bundle cap. Epithelial rings consist of five to eight cells.

General Remarks

Even though the diagram shows spaces between vascular bundles the interfascicular region is highly sclerified,

E. angustifolia var. angustifolia (Fig. 10)

Trichomes and Epidermis

Trichomes thickly cover the stem. In surface view epidermal cells range in length from 53.0 μ to 193.0 μ and average 115.0 μ. Widths of these cells range from 24.0 μ to 40.0 μ and average 33.0 μ. Epidermal cells show a wide range in length which tends to give an irregular pattern. (Fig. 32)

Xylem and Phloem

Features of the xylem include: three to five metaxylem rows, 21 protoxylem points, breadth of vascular bundle 350.0 μ to 450.0 μ.

Pith

Sclerotic cells occur throughout the pith. Sclerified pith cells range in width from 30.0 μ to 59.0 μ and average 44.0 μ. Unsclerified cells are larger and range in width from 31.0 μ to 69.0 μ and average 50.0 μ. The wall thickness (4.0 μ) of sclerortic cells is easily recognized in transectional view. (Fig. 68)

Secretory System

Canals only occur in the cortex. These canals range from 38.0 μ to 45.0 μ and average 40.0 μ in cross diameter. Cortical canals number 26 in transectional view.

General Remarks

Comparatively this species was one of the smaller stems in the genus. Interfascicular regions are sclerified but show no secondary growth. The cortex is largely made up of collenchyma tissue.

General Anatomy of the Petiole

In Echinacea the petiole is supplied by three major collateral vascular bundles a manifestation of departing foliar traces from the stem. But, variations can occur in petiolar anatomy as described by Eames and MacDaniels (1947). Due to different methods of fusion, division, or twisting of the leaf traces, the number of vascular bundles traversing the cortex may or may not be the same number that enter the leaf. In different numbers, minor vascular bundles are associated with the major vascular bundles.

The arrangement of vascular bundles in the petiole is usually constant for a given species and often for families, such as, three for Compositae. In addition, petiole shape can be used as a taxonomic criterion. Transversely cut petioles can be recognized by shapes; horseshoe-shaped, V-shaped, and cylindrical-shaped. Moreover, resin canals, universally present in this genus, differ in size, number, and position in the petiole.

Anatomically, the petiole contains the same tissues as the stem: epidermis, collenchyma in varying amounts, and vascular bundles with associated fibrous sheath. But, as can be seen in E. purpurea and E. sanguinea, the medial

vascular bundle lacks a fibrous cap (Fig. 48,56). Another apparently unusual phenomenon in E. paradosa neglecta is the occurrence of the brachysclerid or stone cell. They appear either isolated, clustered, or in rows. (see Fig. 75) Structurally E. atrorubens is unique the petiole contains three lacunae situated around the medial vascular bundle. (Fig. 47,69)

Petiole Descriptions

E. atrorubens (Fig. 47)

Petiole outline tends to be rounded except for a convex depression on the adaxial side. Each major bundle is associated with two resin canals located one on each side adjacent to the abaxial fibrous cap. The canals that accompany the central vascular bundle are relatively large, 40.0 μ , with five epithele cells. Consequently, they are conspicuous and well differentiated from the surrounding cells. The vascular bundles are almost perfectly rounded and completely ensheathed by fibrous tissue. Air spaces form passageways throughout the length of this petiole. Serial sectioning demonstrated their course as beginning near the stem axis ultimately terminating at the leaf base. Although *E. paradoxa* var. *paradoxa* has air spaces, they appear close to the leaf base. As stated previously, all sections were analyzed from a comparable position, in the case of *E. paradoxa* var. *paradoxa* air spaces occur beyond this point. Besides the major vascular bundles, six minor bundles are present in *E. atrorubens*.

E. sanguinea (Fig. 48)

This species illustrates the change in gross morphology that can occur along the length of the petiole. Close to the stem the petiole is heart-shaped in transection with the ends folded together. Near the leaf base the petiole unfolds allowing reorientation of the margins. Concurrently, transectional views reflect this constant change in petiole structure. Secretory canals are relatively small, 30.0 μ, arranged one on each side of the abaxial bundle cap. Four minor vascular bundles are evident. The medial vascular bundle lacks an abaxial fibrous cap.

E. paradoxa var. paradoxa (Fig. 51)

Of all species studied, E. paradoxa has the thickest petiole. The exaggerated curverture on the abaxial side is discernable even macroscopically. Emphasis here is placed on the secretory system. Canals are comparatively numerous occurring in pairs instead of singly. Spatially as much as 100.0 μ separates each pair of abaxial canals. These are relatively large averaging 40.0 μ in cross diameter.

Toward the abaxial margin of the petiole abundant chlorenchymatous pockets are interspersed among collenchyma tissue. Five vascular bundles are noted in transection.

E. speciosa (Fig. 55)

A striking feature not found in other species is the fan-shaped medial vascular bundle. It has a wide fibrous cap gradually sloping adaxially as the phloem and xylem diminish in lateral extent. Seven vascular bundles can be seen in transection. The canal system is not well developed; in fact, canals associated with the more lateral vascular bundles are greatly reduced in size. Even canals related to the medial vascular bundle are relatively small and inconspicuous measuring 32.0 μ in cross diameter. The tips of the petiole arch upward and give a more or less lunate-shaped outline. Some petioles have loosely arranged parenchymatous tissue orientated adaxially near the epidermis. However, in E. speciosa this area is compacted; the constituent cells have small intercellular spaces.

E. purpurea (Fig. 56)

The petiole is thickened through the medial sector with a gradual flaring and ascending at the marginal ends.

Photosynthetic tissue is scattered among parenchyma cells that make up the abaxial bulge of the petiole. Canals are prominent averaging 45.0 μ when found adjacent to the medial vascular bundle, becoming progressively smaller as lateral vascular bundle size decreases. Five vascular bundles are evident in sectional views; two more are diminutive but recognizable. The central vascular bundle lacks fibrous tissue on the abaxial side.

E. angustifolia var. strigosa (Fig. 50)

The petiole tends to have the outer margins swinging upward slightly. Also, this species has one of the smaller petioles. The "wings" show a leaf-like anatomy made up largely of spongy photosynthetic tissue. Only three vascular bundles supply the petiole. Canals are relatively small, 30.0 μ , sometimes absent from lateral vascular bundles.

E. angustifolia var. angustifolia race intermedia (Fig. 49)

The petiole shows an abaxial convexity which tends to be horizontally flattened on the adaxial surface. A feature readily recongized is the large amount of collenchymatous supporting tissue occupying a position between the

vascular bundles and abaxial epidermis. Medial canals average 38.0 μ in cross diameter. Three major bundles are noted in sectional view.

E. angustifolia var. angustifolia (Fig. 54)

The petiole is somewhat v-shaped with sides not steeply inclined. Outside the lateral vascular bundles an abrupt delimitation of fundamental tissue occurs, continuing as photosynthetic foliar tissue. The canal system is greatly reduced in number; in fact, only one canal 40.0 μ can be seen beside the medial vascular bundle. The minimum of three vascular bundles traverse the petiole. Again, like in E. intermedia and E. angustifolia var. strigosa the petiole is relatively a small structure.

E. laevigata (Fig. 53)

The petiole in cross section appears horseshoe-shaped. Leaves of this species tend to have sheathing bases; this accounts for the lengthy "wings". Fundamental tissue extends to the very end of each wing which fails to show a gradation into foliar anatomy. A uniseriate layer of cutinized cells underlies the epidermis that is structurally

indistinguishable from it. This double-layered tissue forms a definite boundry at the periphery of the petiole. Five vascular bundles are seen in transection. In this species the secretory system is poorly developed except for the medial canals that average 42.0 μ.

E. paradoxa var. neglecta (Fig. 52)

A lunate-shaped outline is closely approximated. Indeed, a greater lateral expansion excentuated by the thiness of the petiole sets apart this species. Canals are well formed (distinct epithelial cells surrounding a large cavity) and larger than can be found elsewhere in the genus. (Fig. 75) Comparatively some of these canals are double the size of even the largest canals of other species. Totalizing all canals present, regardless of size or differentiation, numerically 14 far exceeds counts made for other species. These canals are located typically on the abaxial side of the vascular bundles and some atypically on the adaxial side. Probably this abnormality is due to sheer canal numbers. An unusual arrangement occurs with relation to the medial vascular bundle. Here, pairs of canals were positioned on both the abaxial and adaxial sides.

Well-formed canals range in size from 64.0 μ to 84.0 μ. Noteworthy of mention is an extremely large cavity in all these secretory canals. A range of 31.0 μ to 43.0 μ in cavity diameter was recorded. Accordingly, a well-differentiated ring of epithelial cells surrounds the cavity. Commonly in other species canals are surrounded by four to six epithelial cells but here, between 5 and 15 cells make up the epithelial layer. Furthermore, the epithelial cells have a distinctive shape closely approaching a rectangular or squarish form; while others found in different species usually are elliptic with curved anticlinal walls. Apparently nowhere in the genus occur brachysclerids, or stone cells, except in E. paradoxa var. neglecta. (Fig. 75) These sclerids are conspicuous; their walls being highly refractive makes them appear as shiny, glistening structures. More noticeable was the concentric layering of the walls revealed by a preferential stain. In this case the walls were heavily lignified (stained with safranin) throughout, even the thick secondary walls.

General Leaf Anatomy

It is convenient to recognize anatomical types of leaves. Textbooks refer to the bifacial or dorsiventral leaf, isobilateral or isolateral leaf, and a homogenous mesophyll leaf. However, many leaves show transitional types making it difficult to apply a technical term. In Echinacea, as in many living organisms, certain individuals do not fit the terminology. The only way to circumvent this is to adequately describe leaves of each species.

In comparative studies of leaf anatomy attention is centered on the following: trichomes (kind and frequency), stomata frequency and size, venation patterns, size and shape of vein islets, bundle ends, bundle sheath of veinlets, midrib size, shape, and vascularization, arrangement of palisade and spongy mesophyll, presence of sclerids, crystals, or lignified epidermal cells, margins of leaves, and epidermal imprints. The author regrets that a more detailed study was not completed.

E. purpurea (Fig. 34)

The large veins of this species are evident, especially comparing midribs. The bundle sheath projects abaxially and is more or less rounded. One fan-shaped vascular bundle which lacks a fibrous cap can be seen. No canals appeared in the midvein or lateral veinlets. A strongly bifacial leaf consists of a double tier of palisade tissue and a loosely arranged spongy mesophyl directed abaxially. Trichomes are present which thickly cover the leaf.

E. laevigata (Fig. 35)

A relatively large midrib shows an abaxial convexity. The extremely large vascular bundle lacks a fibrous cap but on each side has small, 30.0 μ canals. The leaf essentially is bifacial in portions, tending to become homogenously elongated The upper surface has two definite rows of palisade tissue. No trichomes are present.

E. speciosa (Fig. 17)

Although having a definite adaxial palisade tissue, this species also has elongated cells abaxially orientated. Throughout most of the leaf the tendency is more bifacial.

A relatively small bundle sheath has the vascular bundle capped on both sides. No canals are present.

E. pallida (Fig. 18)

The most outstanding feature of this leaf is its strong isolateral tendency. Trichomes are abundant covering both upper and lower surfaces of the leaf. Canals are absent in the midrib.

General Anatomy of Petals and Ray Flowers

Petals are essentially leaf-like in form but histologically differ in various ways from the typical leaf. Generally, they show some resemblance in their internal structure to mesophytic or hydrophytic leaves; although often lacking differentiated pallisade and spongy parenchyma tissue.

They consist of ground parenchyma (often called mesophyll), a greatly reduced, branched vascular system, and epidermal layers on the adaxial and abaxial side. The vascular supply (here termed veins and veinlets) usually bifurcates but more noticeably at the tips. Thick-walled supporting tissue often is found surrounding each veinlet. Furthermore, the vascular tissue more than likely will consist of several large veins and a system of smaller veinlets.

Echinacea closely parallels then, the anatomy of most petals; for all the features mentioned previously are exemplified in the ray flowers.

In Echinacea the ground (mesophyllous) tissue is simple in structure, exhibiting homogenity. The thin-walled mesophyllous cells have a central cavity with radiating

interconnected arms. Still, all the cells are loosely arranged into a meshwork of lacunose tissue. (Fig. 82) In transection, the mesophyllous cell cavity is cylindrical elongated in a horizontal plane (running parallel with the vascular system). These mesophyllous cells have outgrowths (arms) that become septate at a point of juncture. Cells so constructed are spoken of as being "armed" by many authors. The arms measure from 28.0 μ to 75.0 μ in length.

Perhaps the most striking feature of the ray flowers are peculiar adaxial epidermal cells modified into various sizes and shapes. The author strongly urges taxonomists to closely examine these cells as possible identifying characters.

Sometimes both epidermal surfaces are papillose but in Echinacea only the adaxial surface exhibits this peculiarity. The inner tangential wall is commonly slightly convex. The outer wall, on the contrary, is often more or less convex or papillose and in (Viola, Nasturium) bear one or more capitate or cone-shaped papillae. Similarly, in Echinacea angustifolia race intermedia the adaxial epidermis partly consists of cells enlarged basally capped

by one or more (never more than three observed) pyramidal-shaped cells. In many plants the anticlinal walls appear either straight, wavy, or may bear internal ridges. The undulation and ridging vary widely in degree of expression in different species. Indeed, the epidermis is less simple than its foliar counterpart.

Due to the weak-walled, complex nature of the adaxial epidermis a dovetailed arrangement seems to permit the greatest mechanical support. The functional importance of these cells is open to conjecture; probably they form a layer mechanically stronger than one of simpler form. Furthermore, in some plants epidermal anticlinal walls along the veins and at the base of the petal are usually straight even if wavy elsewhere. According to some authors variability in wall structure gives an assortment of shapes. In Echinacea, however, the size and shape of adaxial epidermal cells remained somewhat constant for each taxon , at least in the same capitulum.

In Echinacea chromoplasts occur singly in each adaxial epidermal cell and are approximately 8.8 μ in diameter. (see Fig. 86) The abaxial epidermis resembles the typical

epidermal cell having stomata, trichomes, and a heavy cuticular covering (7.0 μ). Adaxial epidermal cells have dense contents containing small particles and chromoplasts. Chromoplasts and pigments in the cell sap occur in any array of colors; from white to a deep pink, as can be seen in the drooping on spreading ray flowers.

Ray Flower Descriptions

E. angustifolia var. strigosa (Fig. 82)

The adaxial epidermal cells are slightly modified into various shapes. Generally these cells tend to be conoidal with round corners. The outer tangential wall is slightly drawn out into a papilla. These cells range from 55.0 μ to 80.0 μ in length and average 55.0 μ. In width these cells range from 48.0 μ to 65.0 μ and average 55.0 μ. Very few, if any, secretory chambers can be found in cross sections. In transection, 13 (veins and veinlets combined) are present. Of these 13 vascular traces only one was a vein in a strict sense of the term. Thick walled supporting tissue accompanied this vein. Trichomes are present on the lower surface of the ray flower. The thickness of the ray flower, including both epidermises, is 265.0 μ.

E. angustifolia var. angustifolia race intermedia (Fig. 83,84)

Adaxial epidermal cells are of two kinds: unicellular and multicellular. The multicellular cells are in tiers mounted on an enlarged basal cell. Cells range from 87.0 μ to

109.0 μ in length and average 100.0 μ. Multicellular cells show a wider range: one pyramidal cell (basal cell 90.0 μ, terminal cell 48.0 μ, overall length 138.0 μ) two pyramidal cells (basal cell 70.0 μ, next cell 39.0 μ, terminal cell 41.0 μ, overall length 150.0 μ) and three pyramidal cells (overall length 308.0 μ). Secretory chambers are present usually on the abaxial side of each veinlet. Secretory chambers range from 40.0 μ to 51.0 μ with the lumen sometimes 30.0 μ wide. A ring of five elliptic epithelial cells surround the canal lumen. In transection 12 vascular strands are present. The ray flower is 286.0 μ thick.

E. atrorubens (Fig. 79,80)

This species is characterized by the short papillae that project from the adaxial epidermal cells. Since the inner tangential wall is extremely wide; these cells have a squatty appearance. The length of these cells ranges from 52.0 μ to 90.0 μ and average 78.0 μ. The basal widths range from 48.0 μ to 72.0 μ and average 55.0 μ. The ray flower is 233.0 μ thick. Secretory chambers are scattered and few in number, often 55.0 μ in cross diameter. In

transection, 12 vascular traces are accompanied by very few abaxial secretory chambers.

E. purpurea (Fig. 81)

Comparatively, E. purpurea has the broadest ray flowers of all the species. Externally the gross morphology reflects this greater size; internally size is expressed by the increased degree of venation. Of the 31 vascular traces in transection, five could be termed veins even though supporting tissue surrounds both veins and veinlets. Trichomes are borne abaxially along each major vein. Abaxial epidermal cells measure 50.0 μ to 68.0 μ in length and average 65.0 μ. In width these cells range from 46.0 to 55.0 μ and average 48.0 μ. Secretory chambers measure 40.0 μ in cross diameter; each canal surrounded by five epithelial cells.

E. laevigata (Fig. 89)

Even the ray flowers lack trichomes demonstrating the glaberosity of this species. The venation pattern consists of 15 vascular traces as seen in transection reinforced by abundant thick-walled supporting tissue. The ray flower,

only 184.0 μ thick, is thinner than in other species. The uniformity in size and shape of the adaxial epidermis is the most obvious character. These cells might be compared to the shape of a 0.38 caliber bullet. In length these cells range from 46.0 to 52.0 μ averaging 47.0 μ. In width these cells range from 28.0 μ to 50.0 and average 35.0 μ. Secretory chambers are apparently lacking or very small.

E. pallida (Fig. 90)

Some irregularity in shape was apparent in the adaxial epidermal cells. They intergrade from the short bullet-shape to a conical or slightly papillose cell. These cells range from 58.0 μ to 82.0 μ in length and average 82.0 μ. Cell width ranges from 46.0 μ to 57.0 μ and averages 48.0 μ. Noticeable macroscopically were trichomes of various lengths. A large amount of thick-walled supporting tissue enveloped the 12 vascular traces. The ray flower measured 235.0 μ in thickness.

E. speciosa (Fig. 87,88)

Relatively, the largest adaxial epidermal cells are found in this species. Lengths range from 83.0 to 125.0 μ

and average 105.0 μ. In width these cells range from 63.0 μ to 78.0 μ and average 75.0 μ. Secretory chambers are present having either four or five epithelial cells. Thickness of the ray flower is 270.0 comprised mostly of the large abaxial epidermal cells. Trichomes are present. Vascular traces number 13 in transection.

E. paradoxa var. neglecta (Fig. 85)

Up till now, the secretory system has shown only one canal situated on the abaxial side of the vascular traces. Here, one or as many as three, secretory chambers are arranged on both sides of the vascular trace. Secretory chambers also occurred throughout the mesophyll tissue. A wide range in size (42.0 μ to 81.0 μ) nearly corresponds to those of the stem, leaf, and petiole secretory systems. Where secretory chambers occur an interior cavity of 50.0 μ makes recognition easy. A ring of three to seven epithelial cells surrounds each cavity. This is in keeping with the many celled epithelial layer found delimiting canals of the stem, petiole, and leaf. In other words, the frequency of the secretory system affects position and arrangement so important as taxonomic characters. Whether or not the

size of these secretory chambers influences the morphology; the fact remains, the ray flower is thicker (more fleshy) in this species. The trichomes are very sparse or absent. Lengths of adaxial epidermal cells range from 59.0 μ to 73.0 μ and average 64.0 μ. They range in width from 45.0 μ to 65.0 μ and average 47.0 μ. Some variability in the outer tangential wall results in sides that are parallel about three-fourths the way up, sloping gradually into a rounded apex. Sometimes they are distinctly papillate (drawn out into a nimple).

E. paradoxa var. paradoxa (Fig. 86)

Again, as in E. paradoxa var. neglecta, a secretory system is well-differentiated in size, frequency, and arrangement. Secretory chambers range from 42.0 μ to 70.0 μ; those associated with vascular traces occur on both adaxial and abaxial sides. Secretory chambers are conspicuous mainly due to their large cavities (40.0 μ) . Lengths of adaxial epidermal cells range from 60.0 μ to 78.0 μ and average 75.0 μ. Widths of these cells range from 44.0 μ to 57.0 μ and average 54.0 μ. Epithelial cell shape resembles E. paradoxa var. neglecta. The thickness of the ray flower is 312.0 μ. In transection 12 vascular traces are present.

E. angustifolia var. angustifolia (Fig. 77)

Thickness of the ray flower is 170.0 μ. Venation pattern consists of 12 vascular traces surrounded by abundant thick-walled supporting tissue. Secretory chambers of four to six epithelial cells are found on the abaxial side of the vascular traces. Most secretory chambers measure 38.0 μ in cross diameter. Adaxial epidermal cells range in length from 56.0 to 67.0 μ and average 58.0 μ. Widths of these cells range from 40.0 to 48.0 μ and average 42.0 μ. The shape approaches a bullet-shape although some cells are slightly pinched in part way up.

E. sanguinea (Fig. 78)

Lengths of adaxial epidermal cells range from 103.0 μ to 135.0 μ and average 105.0 μ. Widths of these cells range from 66.0 μ to 80.0 μ and average 68.0 μ. Structurally these cells characterize the species. An elongate projection (28.0 μ) from a broadened base form what the author terms a "necked" cell. (see Fig. 78) Trichomes are absent. The ray flower is 267.0 μ thick although mostly composed of enlarged adaxial epidermal cells. No secretory chambers are present. Vascular traces number 12 in transection.

Summary of Ray Flower Anatomy

Certainly ecological and genetic factors exert controls that are expressed in the physiology, anatomy, and morphology of any plant. Moreover, parts of a plant, root, stem, petiole, leaf, or flower may be more or less conservative. The flower, and especially petals and ray flowers show greater variational patterns according to some workers. Anatomically, the adaxial epidermal cells are subject to change in the same capitulum or even ray flower. However, where qualitative characters appear, for example, in E. angustifolia race intermedia, E. sanguinea, E. atrorubens, and E. laevigata; they result from a cause and effect relationship. To expect the environment to induce such distinctive epidermal shapes would preclude a fundamental cause, namely heredity. Probably both relatively operate within a range. The author suspects genetic influence as the main cause of these diagnostic shapes.

It is possible then, that E. angustifolia intermedia possesses subtle differences in its genic constitution. This would explain the occurrence of the specialized adaxial epidermal cells found nowhere else in the genus. Not knowing the cause or frequency of such a character in a

colony or species population makes it difficult to interpretate its diagnostic significance. The complexity is further compounded if taken into account that such characters can be governed by a single pair of genes.

Another point worthy of mention is the well-developed secretory system of E. paradoxa var. neglecta and E. paradoxa var. paradoxa. As previously shown in the stem, petiole, leaf, and now the ray flower, a secretory system greatly exceeds in size and frequency that of all other species.

On the basis of the ray flower E. purpurea and E. laevigata are widely separated. In the former the ray flower is broad with a high degree of venation while in the latter the ray flower is narrow with venation reduced.

Summary of Stem Anatomy

The foregoing descriptions of each species analyzed tissue by tissue fails to consider comparative anatomical relationships. Therefore, a composite picture would more nearly reflect the nature of each taxon. It is the intention of the author to elucidate all characters; those mutually shared as well as peculiarities.

Salient features common to all members of the genus (with few exceptions) are:

1. Every species (with the one exception being E. laevigata) is characterized by a kind of trichome. These stem borne uniseriate trichomes are of variable size with three to five septations (Fig. 43,44,45,46) Lenticular markings always appear in the trichome wall. All trichomes are raised on a morphologically distinct area of the epidermis.

2. Below the capitulum the stem is grooved for varying distances, the extent depending on the species.

3. The outer part of the cortical region is modified into chlorenchymatous tissue. This photosynthetic tissue is manifest in the greeness of the stem.

4. Collenchyma, in all cases, consists of thickened walls that abut on intercellular spaces. This is often called tubular collenchyma.

5. Secretory canals are present adjacent to and originate through the division of, the endodermis. All species have secretory canals located either opposite the vascular bundle caps and/or interfascicular region. In the pith, secretory canals occur usually opposite protoxylem points except where absent altogether as in E. angustifolia race intermedia, E. angustifolia var. strigosa, E. angustifolia var. angustifolia and E. sanguinea.

6. Each species exhibits a distinct, continuous endodermal layer or layers. A carbohydrate, presumably starch, is confined mostly to the endodermal tissue. Structurally, the starch grains appear all alike. They are granular seemingly with roughened surfaces.

7. Tissue systems lack crystals of any type.

8. Collateral vascular bundles are arranged in a ring (dictyostele or siphonostele where secondary growth is initiated.) An integral part of the vascular bundles are the crescent-shaped bundle caps.

9. As seen in maceration, xylem elements consist wholly of spiral, scalariform, and reticulate vessels, xylem parenchyma, fibers but no tracheids. Tracheidless vascular tissue is not uncommon in the highly specialized families such as the Compositae.

10. The nodal configuration is prolongated into three foliar traces sometimes termed trilacunar when accompanied by three leaf gaps.

11. Throughout the genus occurs one stomatal type, the anomocytic or irregular celled type. (Fig. 27,32)

Eames and MacDaniels states:

> "In the various organs and parts of plants, the vascular tissue differs in arrangement, position, and method of attachment from those of other organs or parts of organs, and these differences are constant and characteristic. The skeleton of a species has a definite and fixed plan and differs more or less from that of other species. The skeletons of the larger groups of plants differ from one another in important respects; the skeletons of smaller groups differ in less important respects but may be varied in structure."

Thus the variation in primary stem structure of different species is based on differences in relative distribution of the vascular and fundamental tissue.

All measurements and subsequent evaluation of anatomical affinity is based mostly on stelar patterns. Considerations of all stem characters: stem diameter, trichomes, epidermal size and patterns, cortical breadth, pericyclic fibers, phloem, size of xylem elements, metaxylem rows, number of protoxylem points, radial extent of largest and smallest vascular bundle, diameter of pith, dimensions of pith cells and secretory system has enabled the author to segregate certain species into structually similar groupings. For discussion and organizational purposes the author considers five anatomical complexes. How well this anatomical information substantiates genetic data is open to argument.

Complex No. 1

(*E. laevigata*, *E. purpurea*)

E. laevigata and *E. purpurea* in stem diameter, are the largest relatively of all species studied. As the diagram illus-

trates, vascularization and spatial distances of tissue systems compare favorably. So much so, that except for the legend it is practically impossible to distinguish one from the other. The secretory system is related in development, position, and size. Cortical tissue in both species is composed primarily of parenchyma. The dermal system differs in the presence and absence of trichomes and in epidermal cell size. Morphologically then, this complex might seem to be unrelated, but anatomically each is closely related.

Complex 2

(E. pallida, E. speciosa)

Both of these species show secondary growth; however, in E. pallida all interfascicular regions are initiating secondary growth. In E. speciosa secondary growth lags farther behind with some of the medullary rays distinct. Features listed as criteria for stem analysis correspond in each species. The secretory system is not well developed in either species. Unlike E. speciosa, E. pallida has thin-walled accessory tissue situated around pith canals. Striking similarity in leaf midrib structure strengthens

this complex. The dermal system agrees in trichome frequency, epidermal size, and pattern.

Complex 3

(*E. atrorubens*; *E. paradoxa* var. *paradoxa*, *E. paradoxa* var. *neglecta*)

The dermal system unites members of this complex. All members have sparsely pubescent stems. Furthermore, epidermal patterns and measurements closely parallel one another. The stem diameter and vascular skeleton compares favorably in several characters. Canal size and position are closely related; moreover, the kind of canal in *E. atrorubens* and *E. paradoxa* var. *neglecta* (a many celled epithelial ring delimiting a large cavity) significantly corresponds. The author wishes to point out *E. atrorubens* does have thin-walled accessory tissue elsewhere recorded in *E. pallida*. Each member of this complex can be separated easily not by one but several anatomical characters. Of special interest is the sharp distinction between *E. paradoxa* var. *neglecta* and *E. paradoxa* var. *paradoxa*. On the other hand, strong similarity in ray flower anatomy is exhibited by *E. paradoxa* var. *neglecta* and *E. paradoxa* var. *paradoxa*.

Complex 4

E. angustifolia race intermedia, E. angustifolia strigosa, E. angustifolia var. angustifolia

This complex is more unified by similar characters than others. The author examined many specimens in the field and herbarium; which always showed sclerified pith. The height of the stem, at which sclerotic cells diminish and finally are lost varies somewhat. Sometimes in E. angustifolia var. strigosa and E. angustifolia var. angustifolia sclerotic pith tissue can be found only six to twelve inches above ground level, in E. angustifolia race intermedia, however, this may reach a height of two or more feet. The pith of all members has a black substance that fills the intercellular spaces. In longitudinal section, this appears as long dark streaks between the unsclerified pith cells. All members lack a canal system in their pith. Stem size and vascularization follows the same general plan. The cortex of all members is made up largely of collenchyma. The dermal system, of trichomes and epidermal cells vary slightly. Actually E. angustifolia var. strigosa and E. angustifolia are so much alike not a good single character will separate them.

Complex 5

(*E. sanguinea*)

E. sanguinea shares certain characters yet lacks others found in complex four. For instance, the pith lacks canals and sclerotic cells. Individual pith cells average much larger in width than members of complex four. The stem is relatively small with a small fraction of vascularization. Possibly the nearest relative is a member of complex two or three. The dermal system resembles members of complex three and four. Trichomes are abundant, more like complex two and four. There is so much overlap into several other complexes that it is best to treat *E. sanguinea* separately.

GENERAL KEY

Combining Anatomical Characters of the Stem, Petiole, and Ray Flowers

1a. Canals present in both pith and cortex ..... (2)

2a. Stem relatively larger (diameter 4.5 to 5.5mm.); protoxylem points over 42; secretory canals originating opposite vascular bundles and interfascicular region adjacent to endodermis ..... (3)

3a. Trichomes present on stem ..... E. purpurea

3b. Trichomes absent from stem .... E. laevigata

2b. Stem relatively smaller (under 4.5mm.) protoxylem points less than 42; secretory canals originating opposite interfascicular region adjacent to endodermis ..... (4)

4a. Stem epidermis consisting of rectangular cell with mostly straight walls..... (5)

5a. Petiole with three air spaces around medial vascular bundle ---------- E. atrorubens

5b. Petiole lacking air spaces ..... (6)

6a. Petiole with stone cells ..... E. paradoxa var. neglecta

6b. Petiole without stone cells ..... E. paradoxa var. paradoxa

4b. Stem epidermis consisting of irregular sided cells with mostly oblique walls ..... (7)

7a. Stem showing strong secondary growth throughout ... E. pallida

7b. Stem showing slight or no secondary growth throughout ..... E. speciosa

1b. Canals present only in cortex ..... (8)

8a. Sclerotic cells scattered throughout pith..(9)

9a. Ray flowers with abaxial epidermal cells of two kinds; unicellular and multicellular ..... E. angustifolia var. angustifolia race intermedia .....

9b. Ray flowers with adaxial epidermal cells all unicellular ..... *E. angustifolia* var. *angustifolia*, *E. angustifolia* var. *strigosa*

8b. Sclerotic cells absent; pith parenchymatous. . *E. sanguinea*

A Key Based on Marginal Ray Flower Anatomy

1a. Epidermal cells on adaxial surface of two kinds; multicellular, consisting of an enlarged basal cell and a catenuliform series of 1, 2, or 3 discrete pyramidal cells; and unicellular, papillose cells that average 100.0 μ in length ..... E. angustifolia var. angustifolia race intermedia

1b. Epidermal cells on adaxial surface all unicellular; either papillose, conical, or bullet-shaped ..... (2)

2a. Veinlets as seen in cross section number 31±1 with extensive supporting tissue; adaxial epidermal cells average 65.0 μ in length and 48.0 μ in width; trichomes present .. E. purpurea

2b. Veinlets as seen in cross section between 12 and 16 ..... (3)

3a. Epidermal cells on adaxial surface uniform in shape whether conical or bullet-shaped; average lengths range from 47.0 u to 75.0 u average widths range from 35.0 u to 55.0 μ; papillary cells lacking ..... (4)

4a Epidermal cells on adaxial surface uniform in size and shape; average length 47.0 u and average width 35.0 u; these cells bullet-shaped showing convexity in outer tangential walls; trichomes absent ..... E. laevigata

4b. Epidermal cells on adaxial surface more variable in size; average lengths 58.0 μ to 80.0 μ and average widths 42.0 μ to 55.0 μ; trichomes present but sparsely so in E. paradoxa var. neglecta and E. paradoxa var. paradoxa ..... (5)

5a. Secretory chambers relatively abundant; positioned not only on abaxial side of vascular traces but scattered throughout mesophyll; secretory chambers ranging in size from 42.0 μ to 81.0 μ; concial-shaped adaxial epidermal cells ..... E. paradoxa var. paradoxa, E. paradoxa var. neglecta

5b. Secretory chambers not abundant and always on the abaxial side of vascular traces; secretory chambers greatly reduced in size, under 40.0 μ or absent ..... E. angustifolia var. angustifolia E. angustifolia var. strigosa

3b. Epidermal cells on adaxial surface highly variable in shape and when not so conspicuously papillose; relatively larger in average lengths (70.0 μ to 125.0 μ) and in widths (48.0 μ to 75.0 μ) .. (6)

6a. Epidermal cells on adaxial surface variable in size and shape; generally conical; length range from 58.0 μ to 83.0 μ; trichomes abundant; apparently secretory chambers lacking or greatly reduced in size ..... E. pallida

6b. Epidermal cells on adaxial surface average from 78.0 μ to 125.0 μ in length; forming papillary projections except in E. speciosa ..... (7)

7a. Epidermal cells on adaxial surface broad at base with short papillae; average length 78.0 μ and average width 55.0 μ ..... E. atrorubens

7b. Epidermal cells on adaxial surface not broad at base with long distinct papillae or over 90.0 μ in length .... (8)

8a. Epidermal cells on adaxial surface with elongate papillae "necked" ..... E. sanguinea

8b. Epidermal cells on adaxial surface not as above ..... E. speciosa

A Key to Species of *Echinacea* Based Solely on the Stem Secretory System

(The position, number, and size of canals serve as diagnostic characters)

1a. Canals present in both pith and cortex ..... (2)

2a. Pith canals oversized; some exceeding 55.0 μ with conspicuous cavities (28.0 μ to 45.0 μ); epithelial lining consisting of 6 to 14 cells ..... *E. paradoxa* var. *paradoxa*, *E. paradoxa* var. *neglecta*

2b. Pith canals usually smaller than 55.0 μ .. (3)

3a. Cortical canals appearing directly opposite vascular bundles and interfascicular region; numerically more abundant exceeding 45 as seen in transverse section; pith canals with a single canal positioned opposite protoxylem points; not in pairs; sometimes one canals along each side of vascular bundle; accessory thin walled tissue absent ..... *E. laevigata*, *E. purpurea*

3b Cortical canals appearing opposite interfascicular region; numerically less abundant under 45; pith canals more commonly in pairs, tending to anastomose in *E. pallida*; Accessory thin-walled tissue present accept in *E. speciosa* ..... (4)

4a Accessory thin-walled tissue accompaning canals of pith either in juxtaposition or overunder arrangement; more rarely replacing the canal in the same morphological position ..... (5)

5a. Canals of pith numerous tending to anastomose; others paired side by side or overunder arrangement; seemingly a bizarre pattern ..... E. pallida

5b. Canals of pith relatively large averaging 46.0 μ discrete not anastomosing, usually a solitary canal opposite protoxylem points with some vascular bundles lacking canals; a paucity of pith canals approximately 20± as seen in transectional view ..... E. atrorubens

4b. Accessory thin-walled tissue absent in pith; canals predominately grouped in pairs opposite protoxylem points. ... E. speciosa

1b Canals present in cortex only . . .. (6)

6a. Canals of cortex never number more than 16 as seen in transection .... E. sanguinea

6b. Canals of cortex always number more than 16 as seen in transection .... E. angustifolia var. angustifolia E. angustifolia var. strigosa E. angustifolia var. angustifolia race intermedia

CONCLUSIONS

Eleven different entities within the genus Echinacea were analyzed anatomically. On the basis of comparative studies using the stem, petiole, leaf, and ray flower, five natural groupings were recognized. The author prefers to consider each group as an anatomical complex showing related affinities. Each complex is represented as follows:

(1) E. purpurea, E. laevigata

(2) E. pallida, E. speciosa

(3) E. atrorubens, E. paradoxa var. neglecta,
E. paradoxa var. neglecta

(4) E. angustifolia var. angustifolia,
E. angustifolia var. strigosa
E. angustifolia var. angustifolia
race intermedia

(5) E. sanguinea

This scheme, based primarily on the stem, has its finer distinction drawn from the petiole, leaf, and ray flower anatomy.

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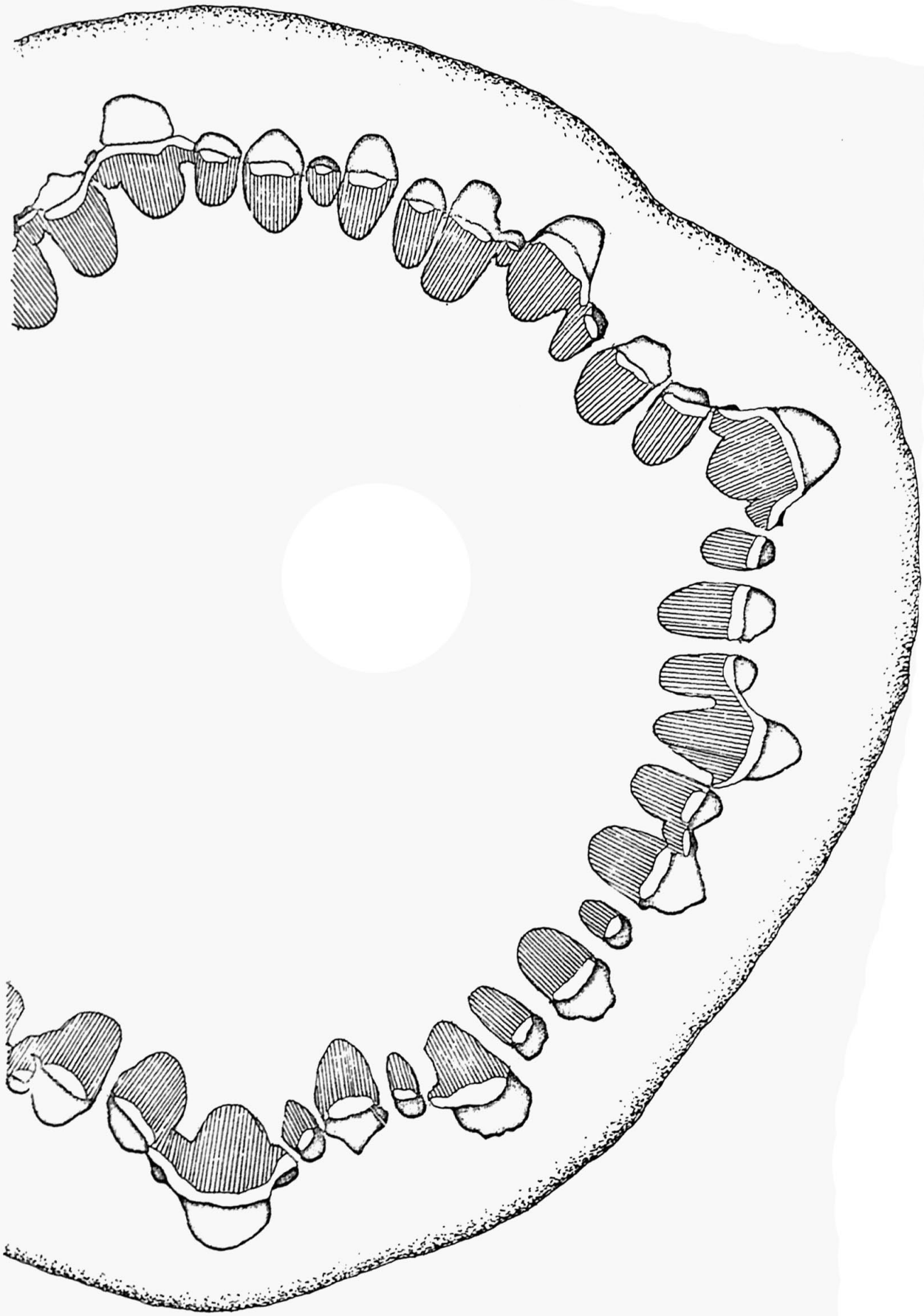


Fig. 1

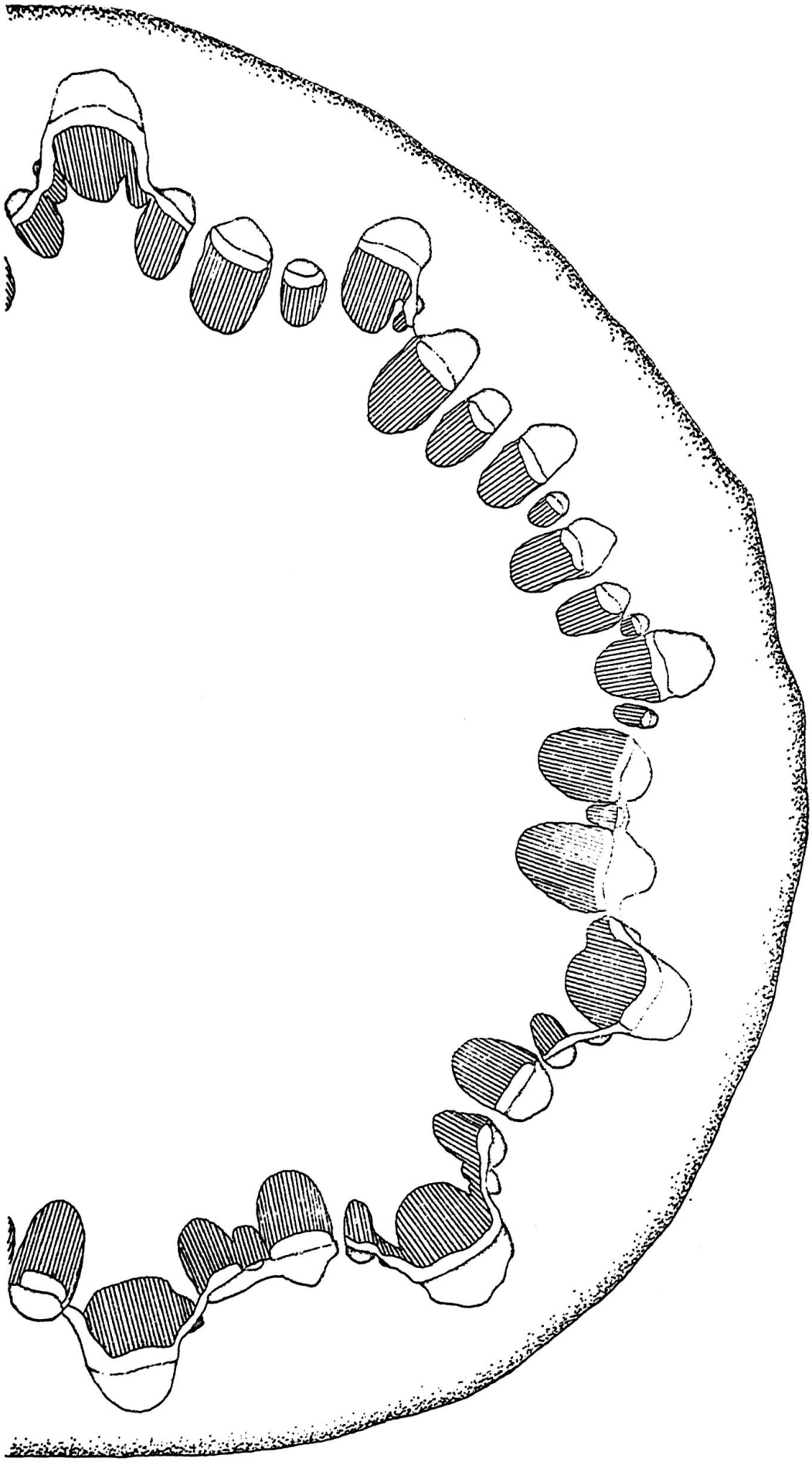


Fig. 2

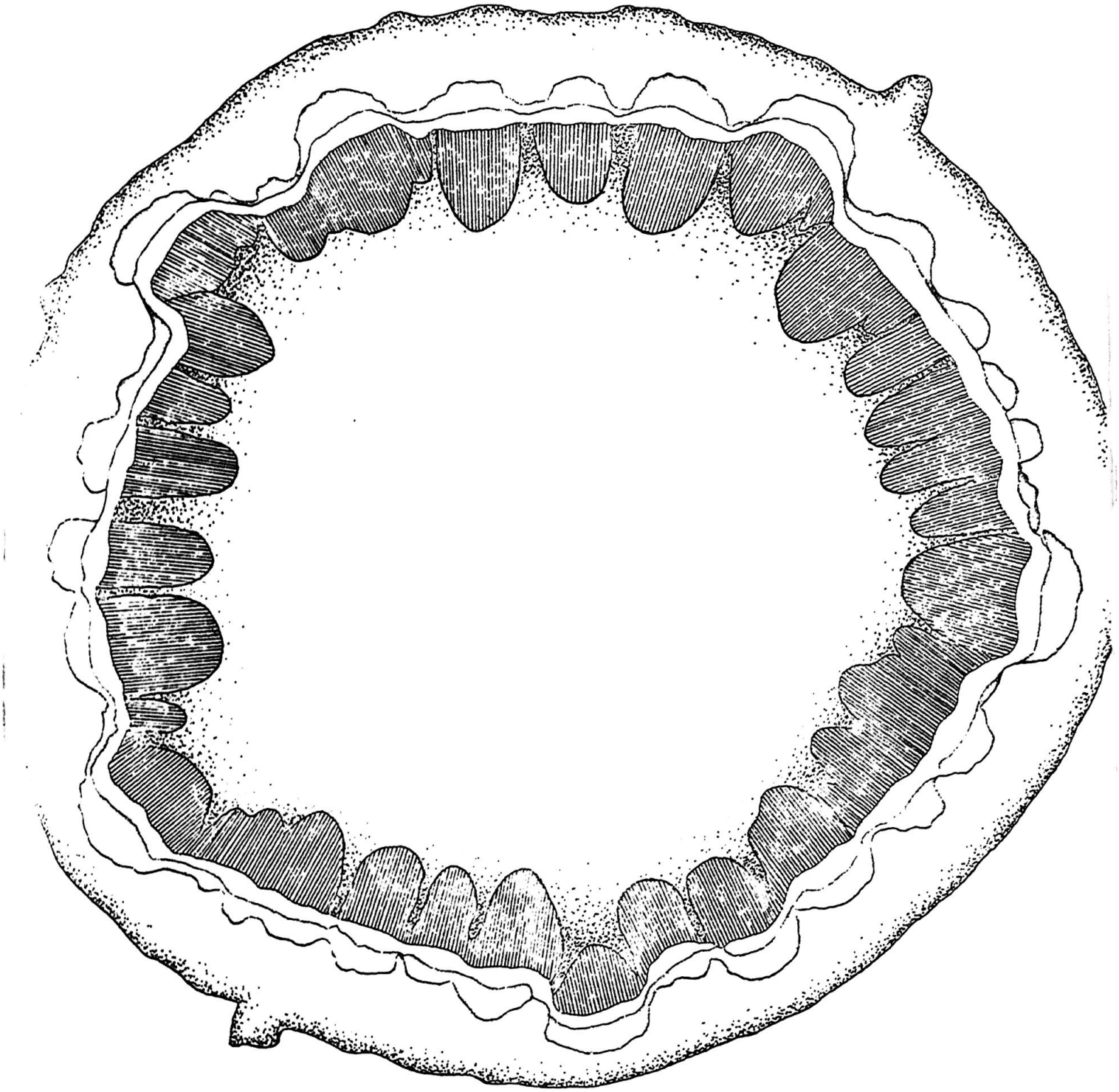


Fig. 3

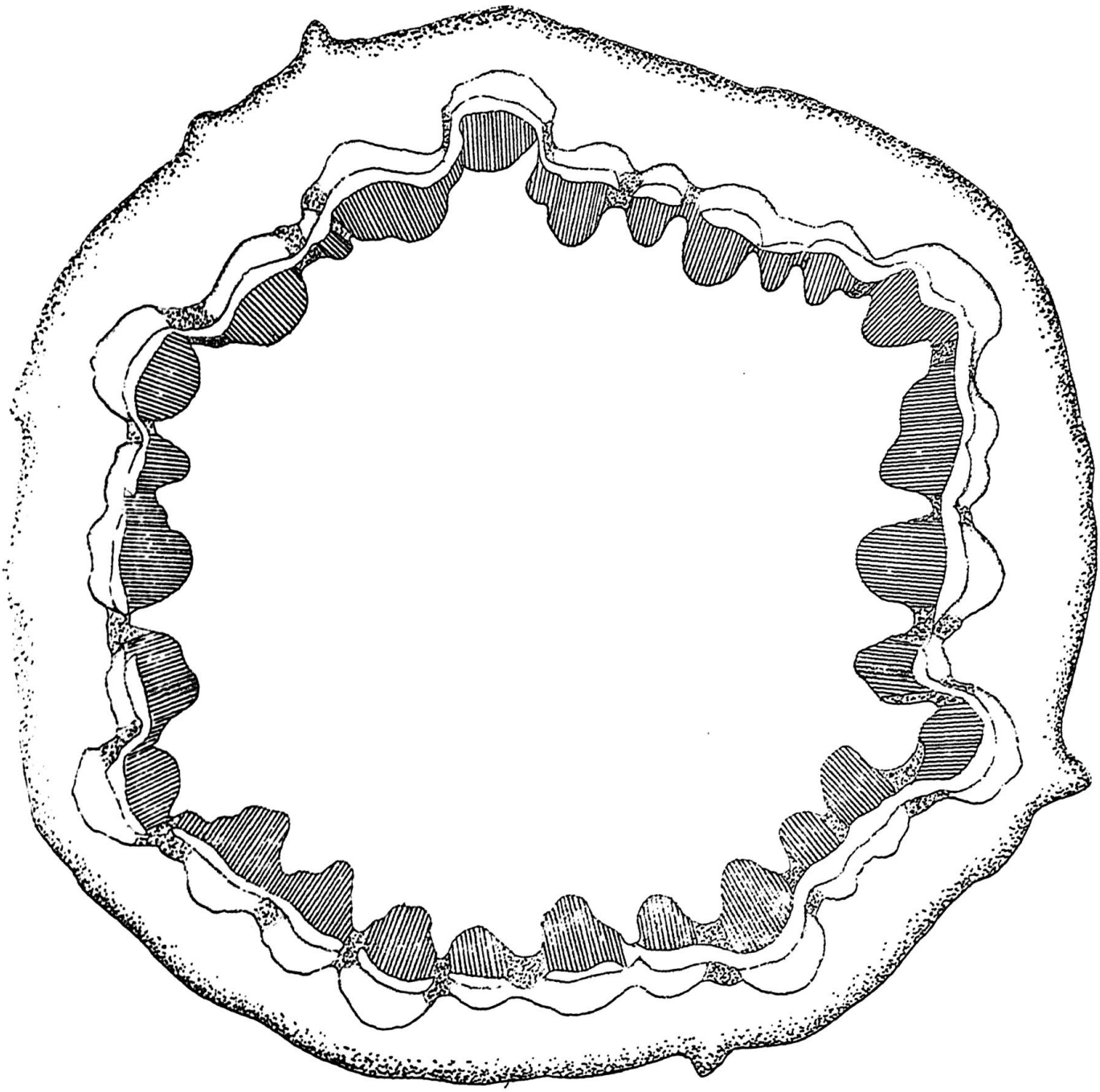


Fig. 4

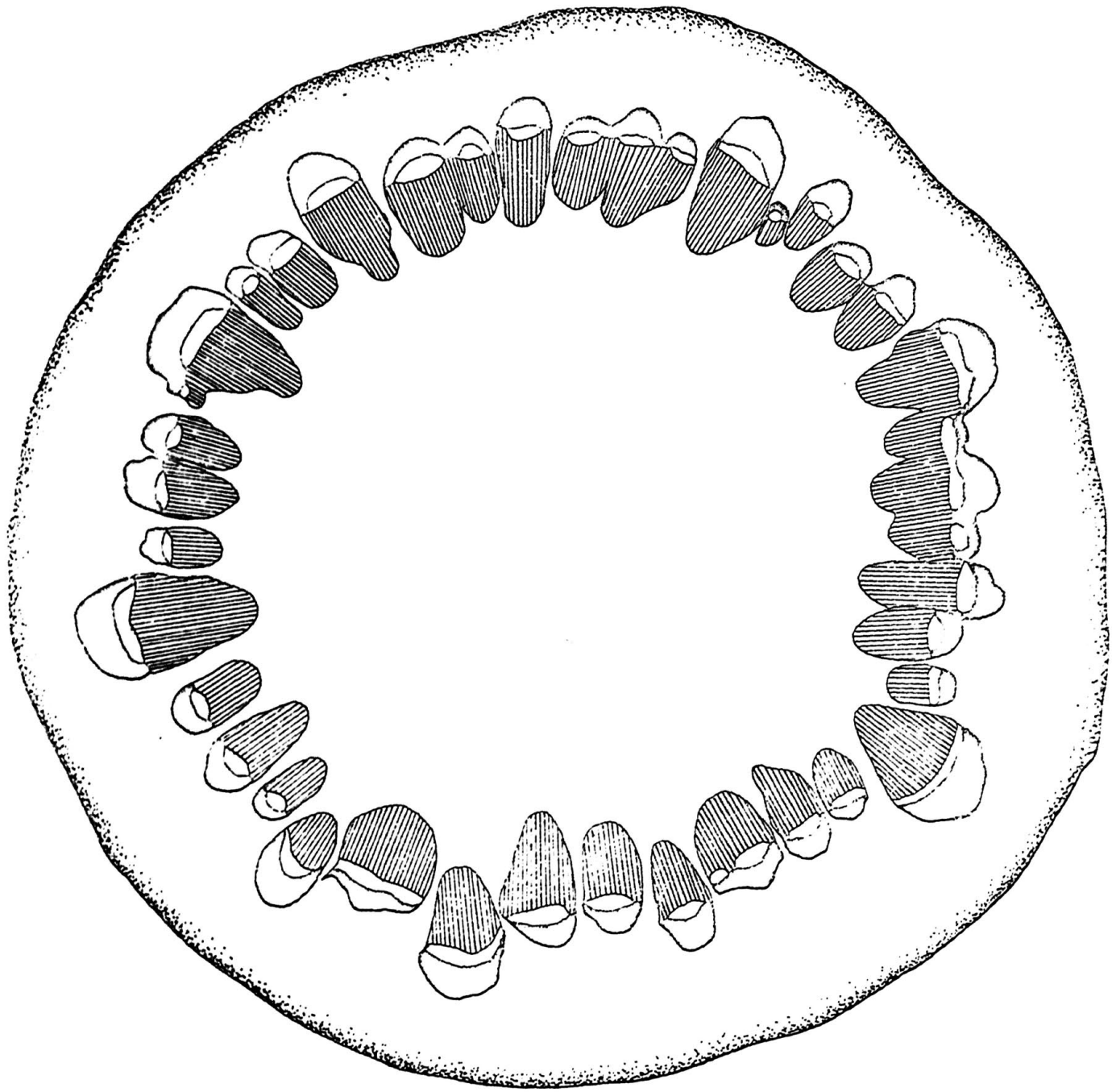


Fig. 5

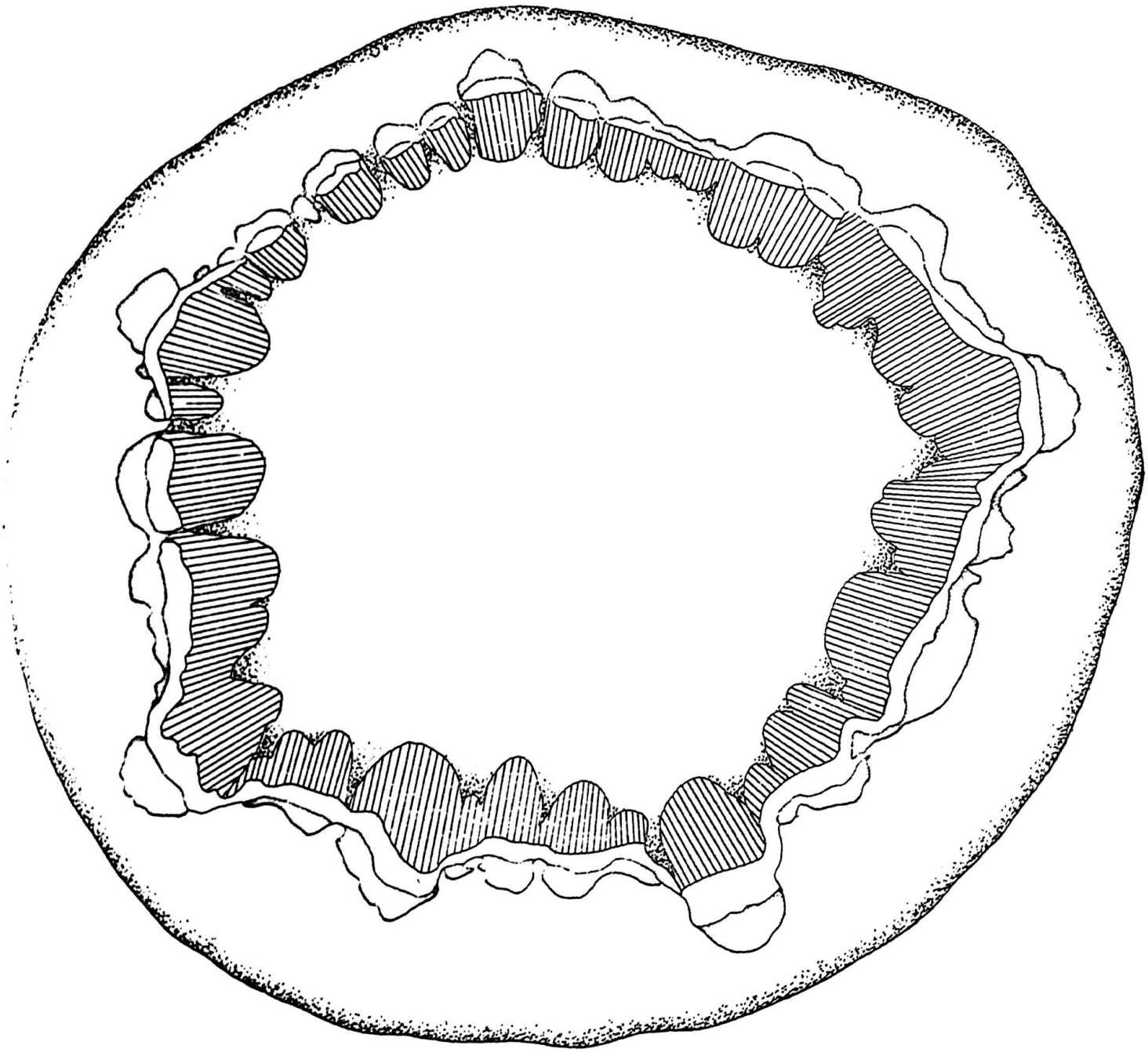


Fig. 6

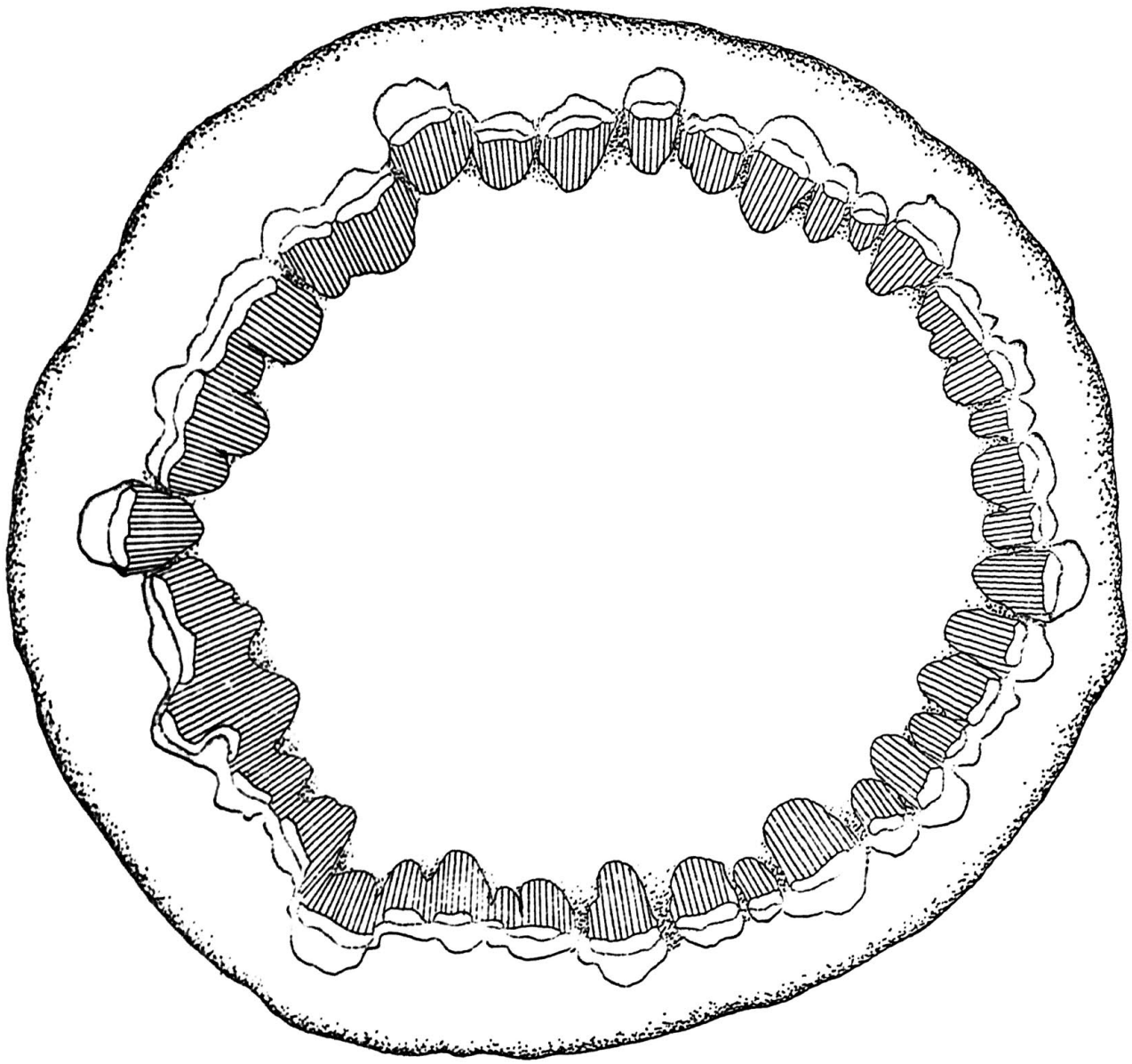
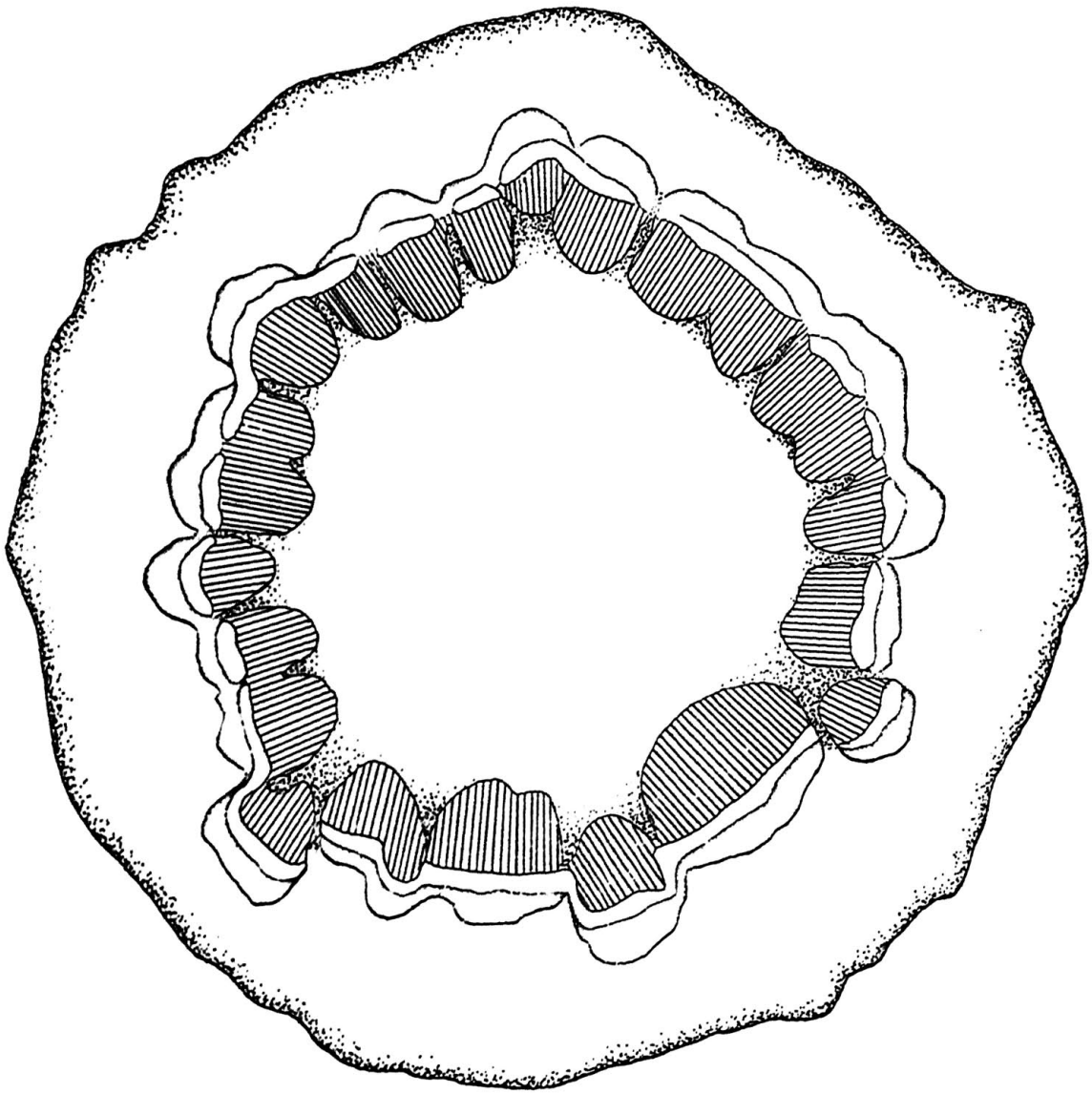


Fig. 7



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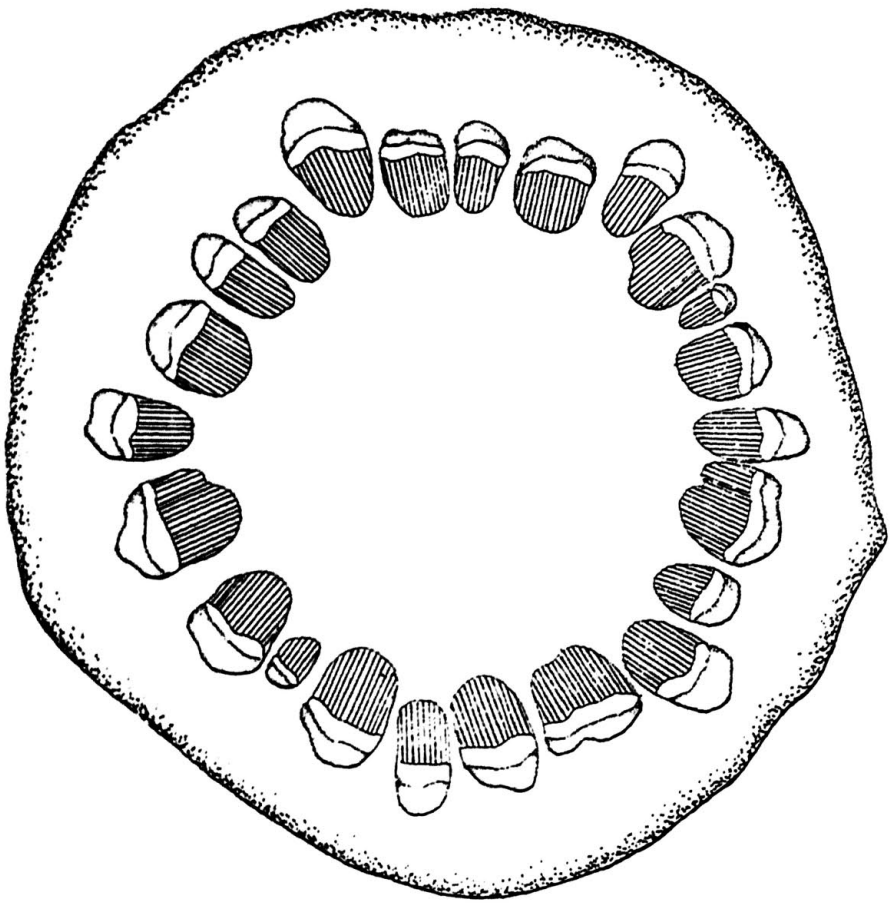

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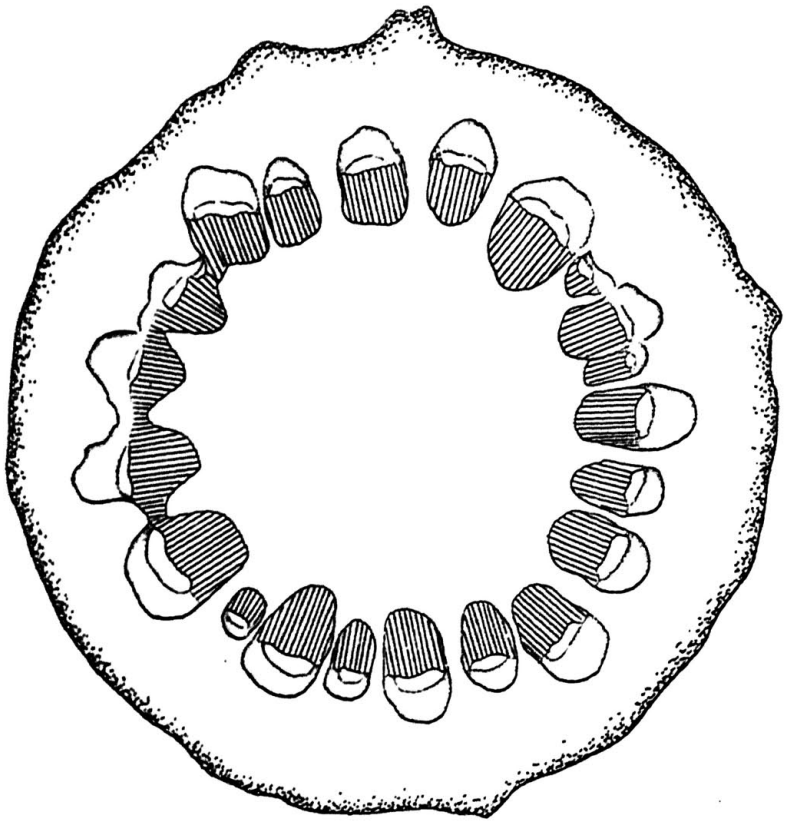

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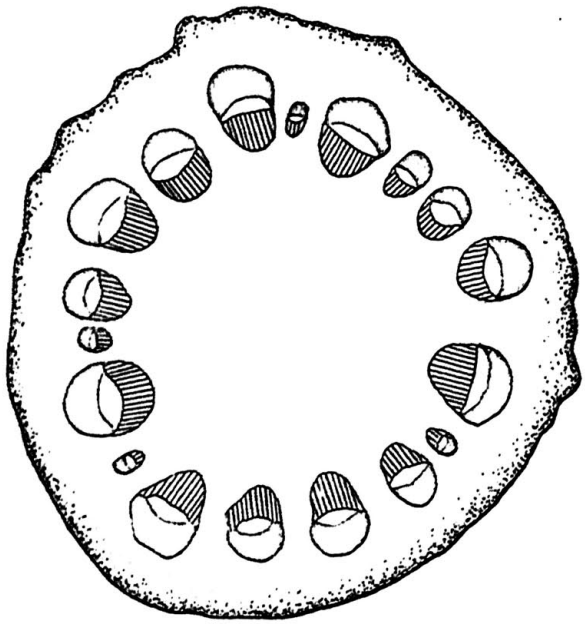

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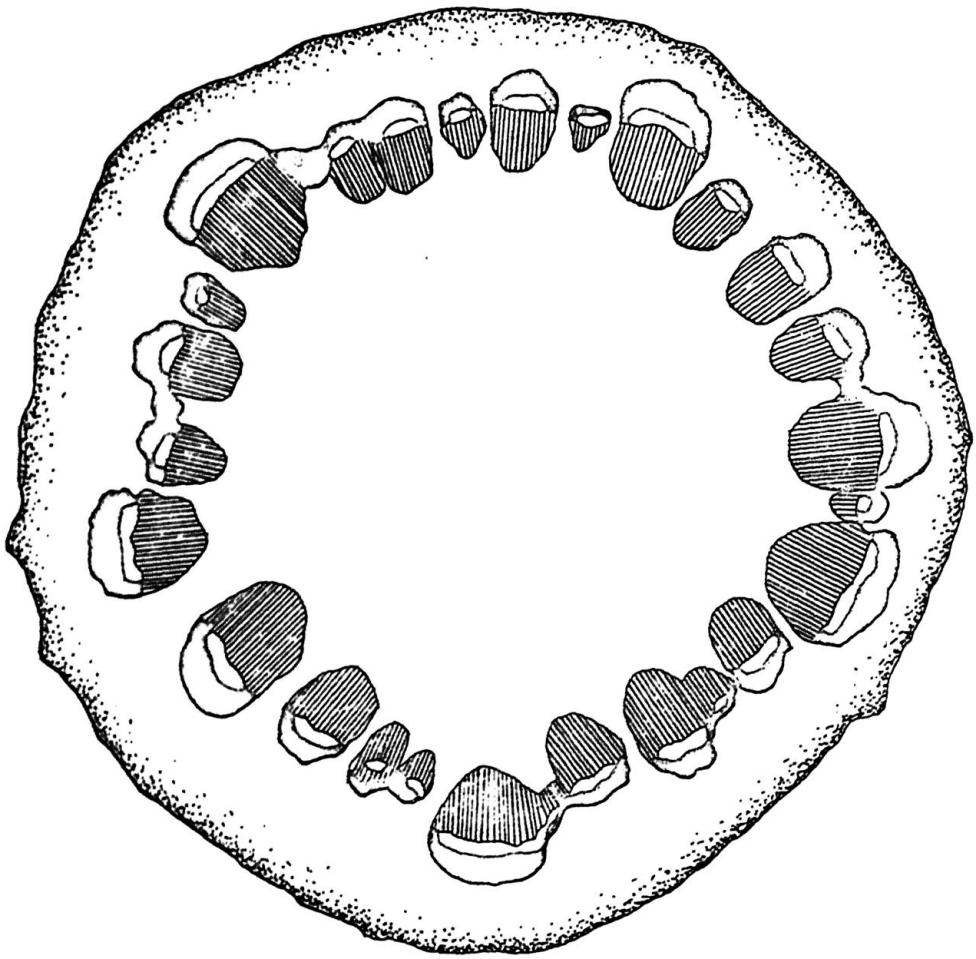

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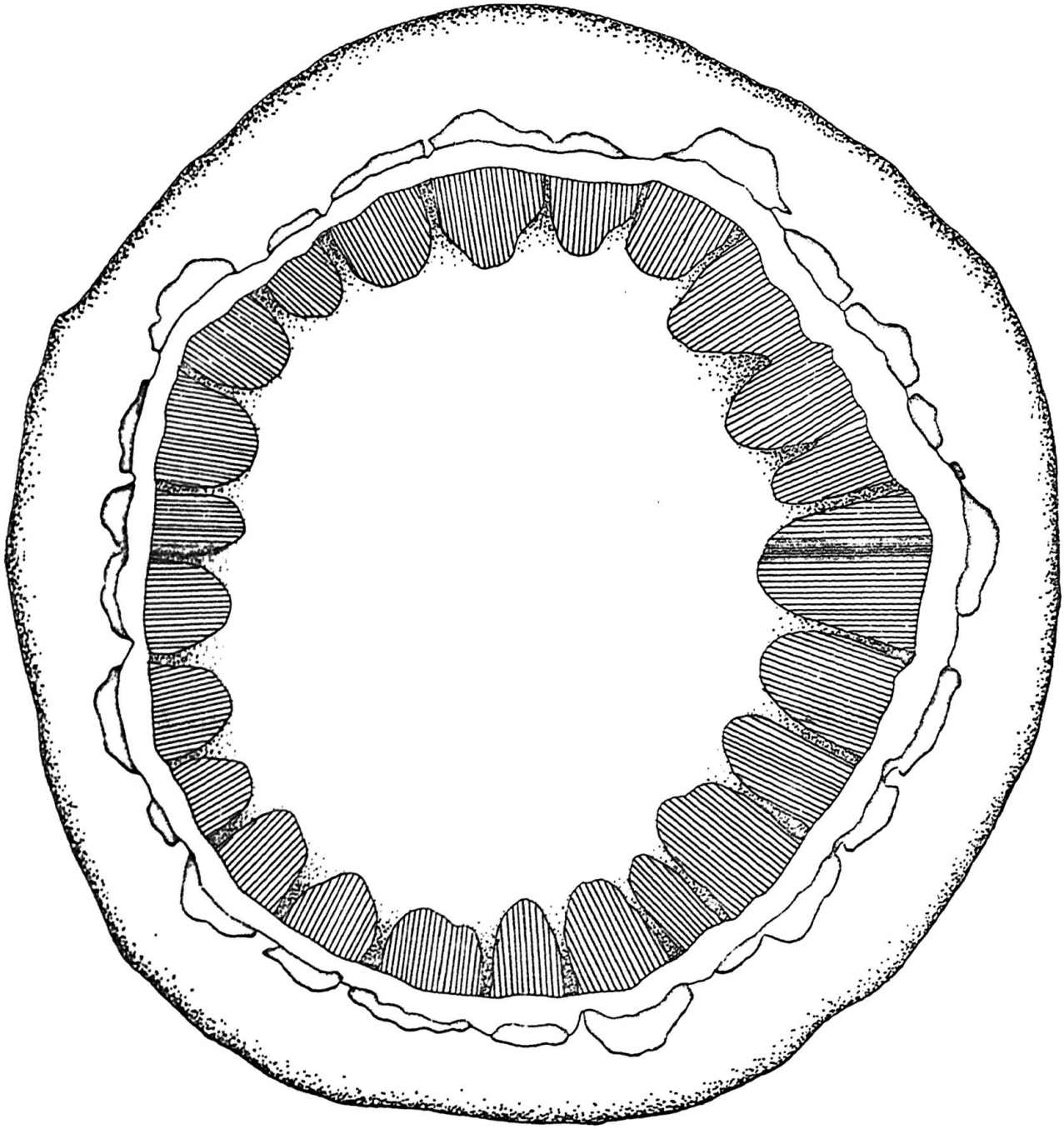

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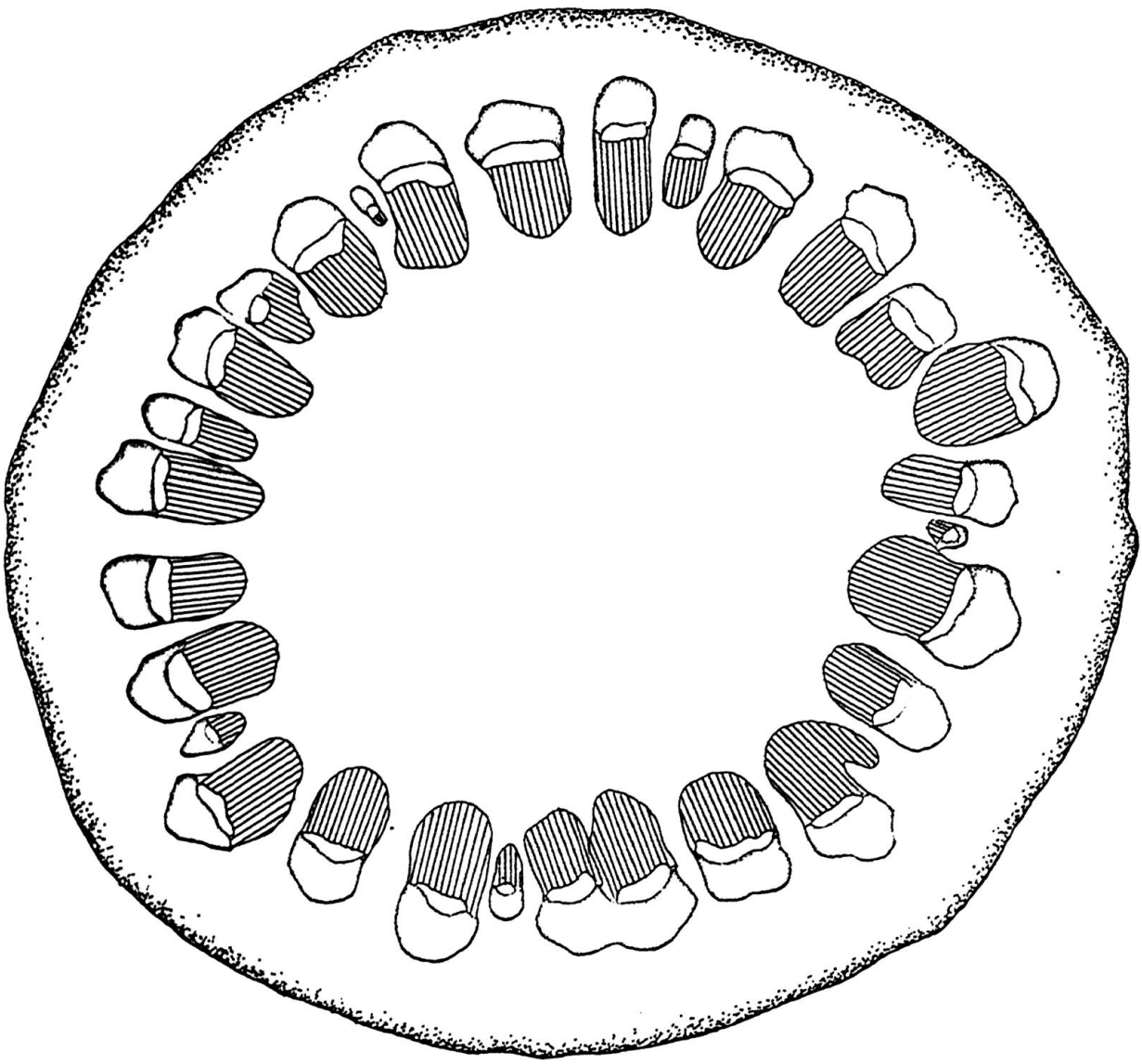

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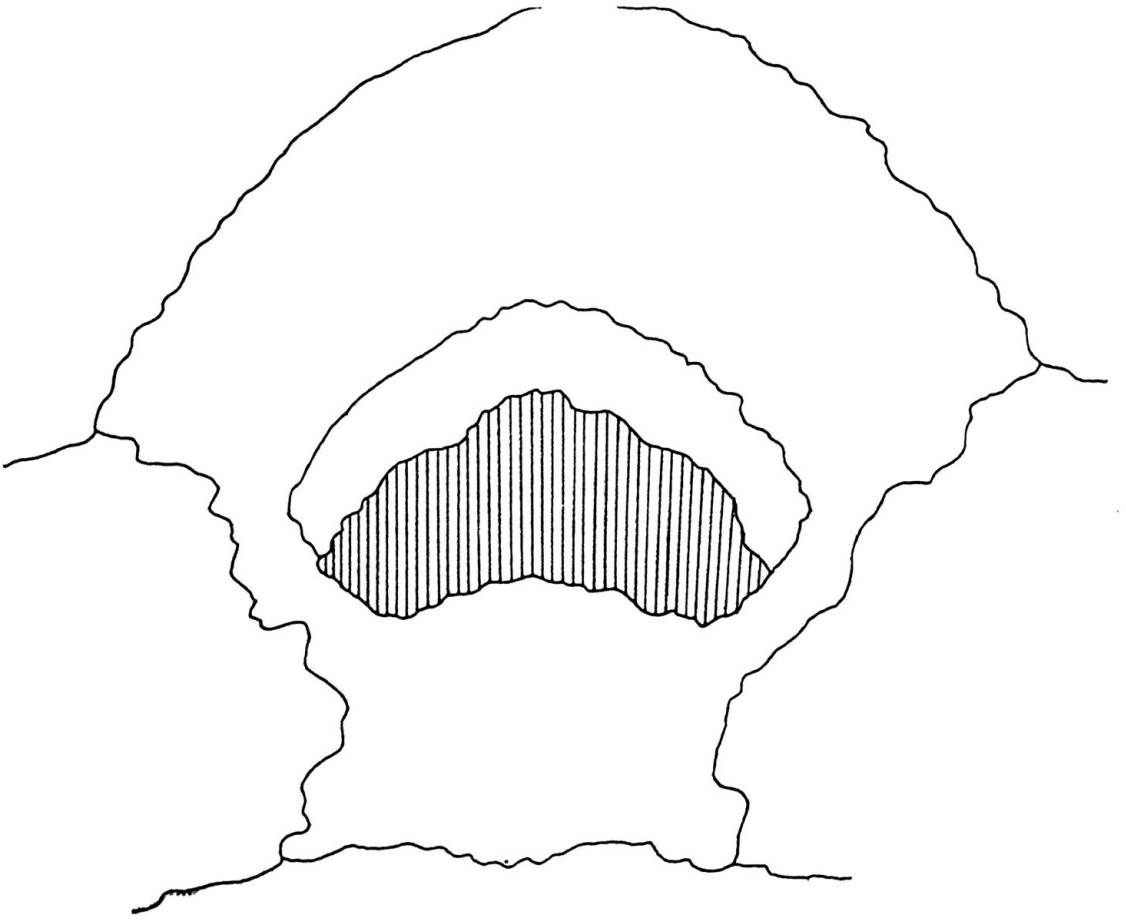

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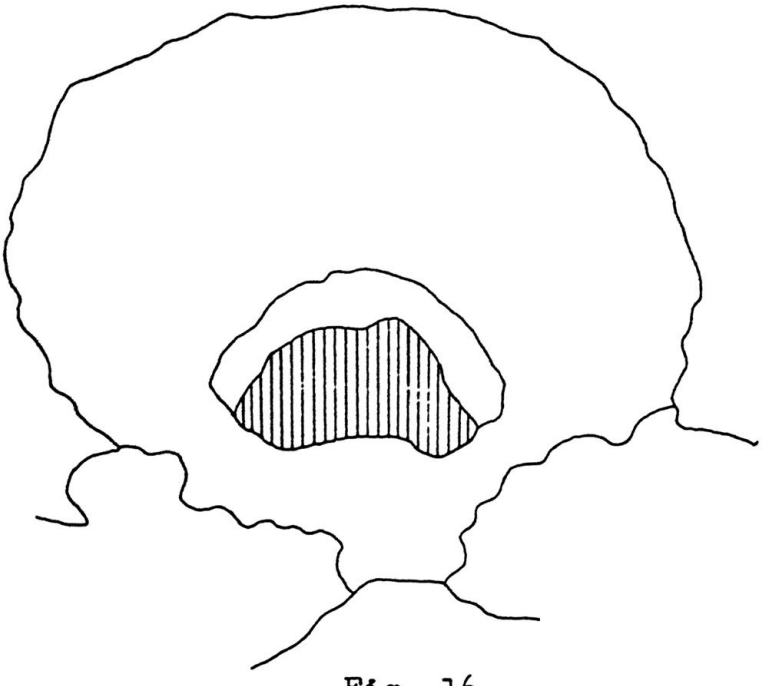

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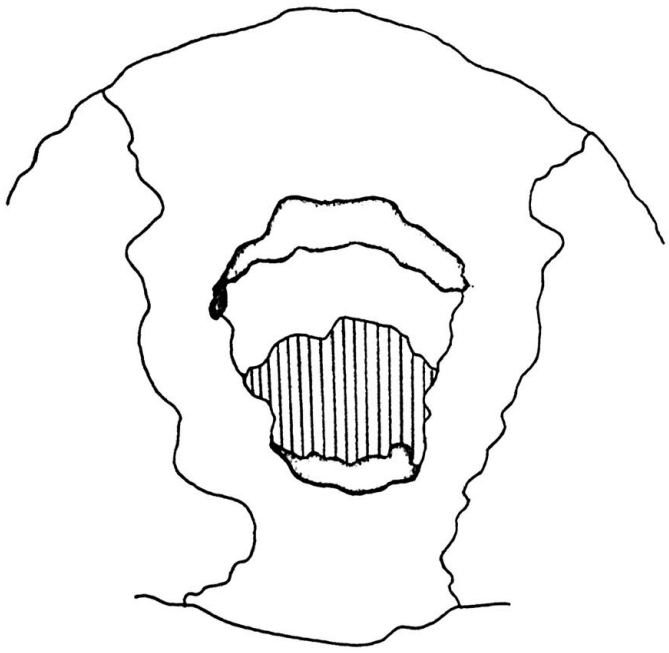

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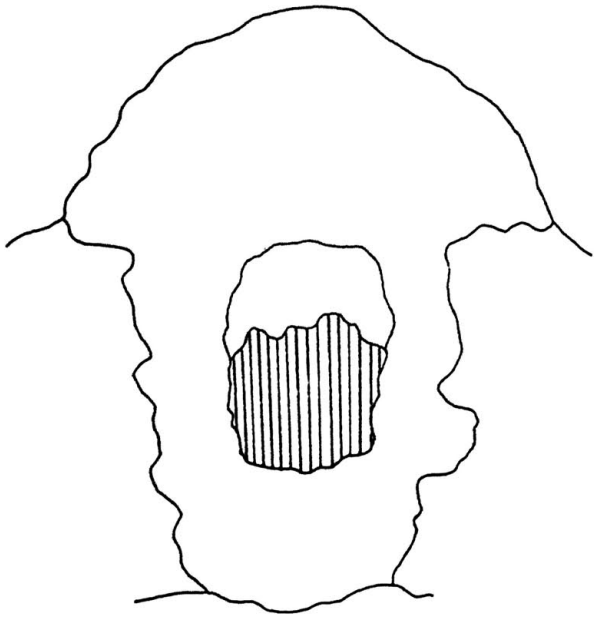

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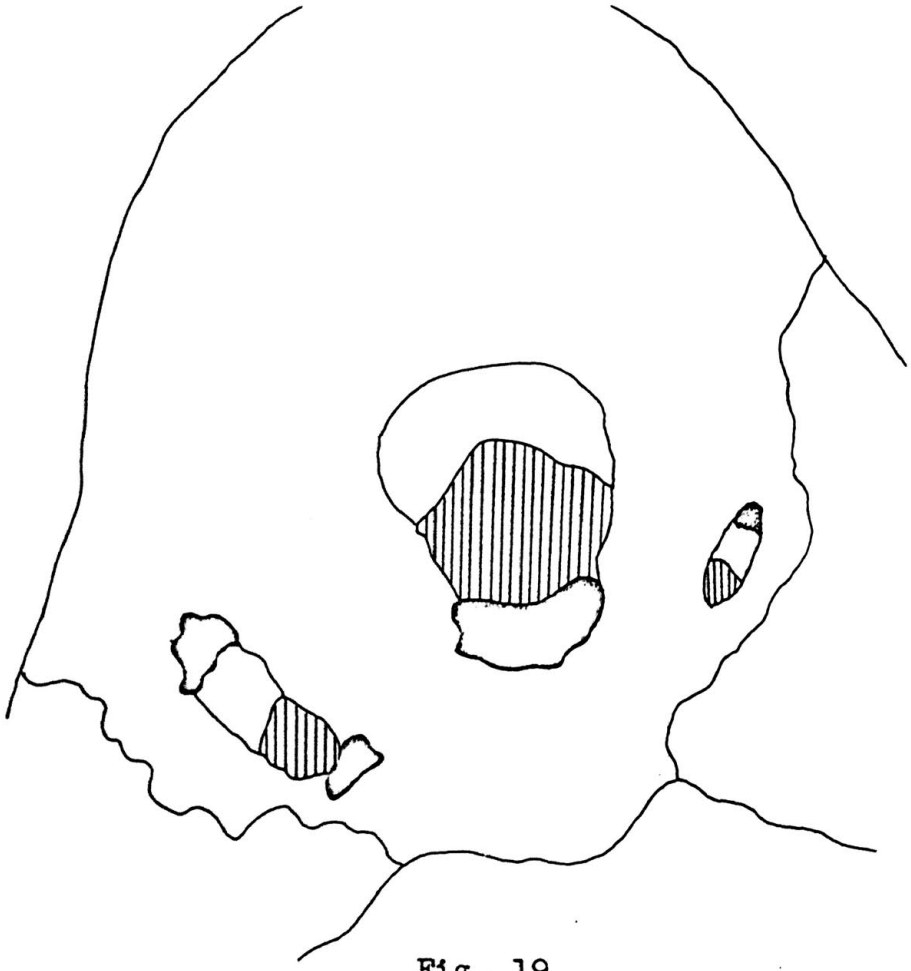

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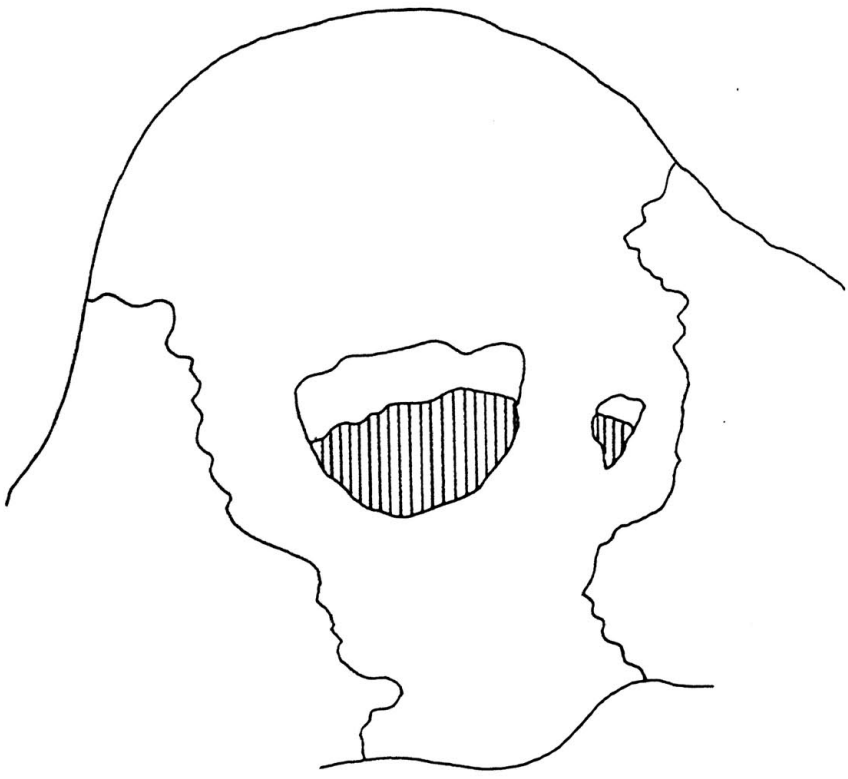

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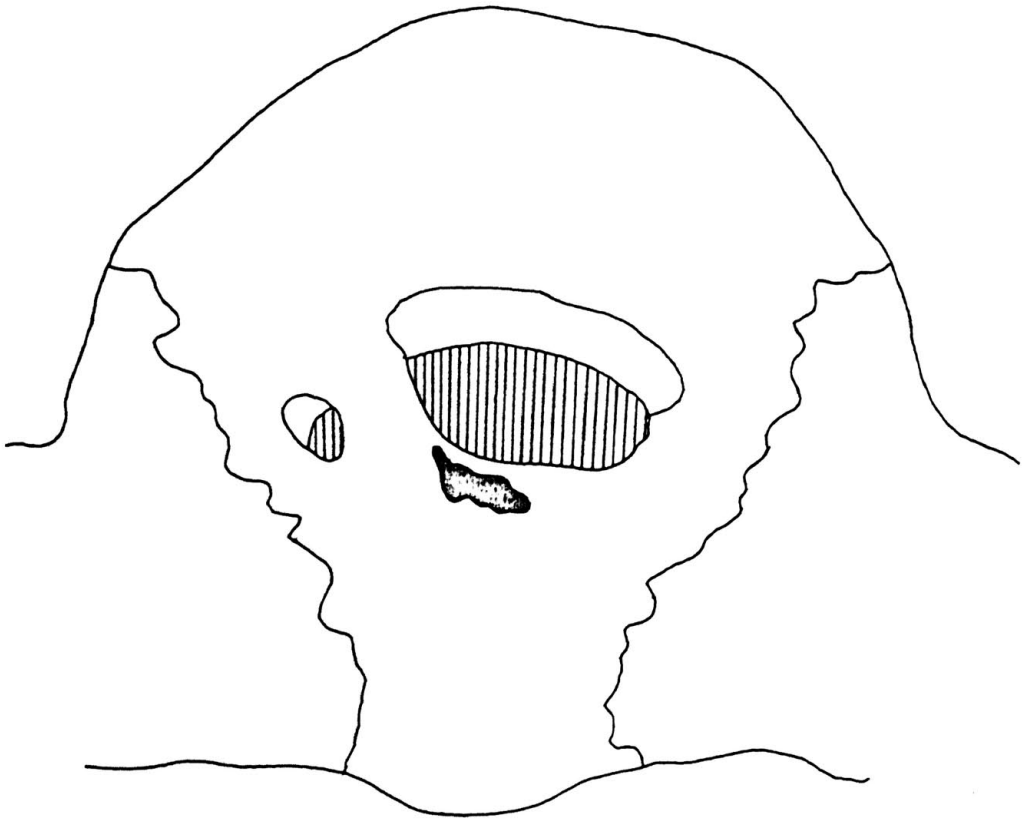

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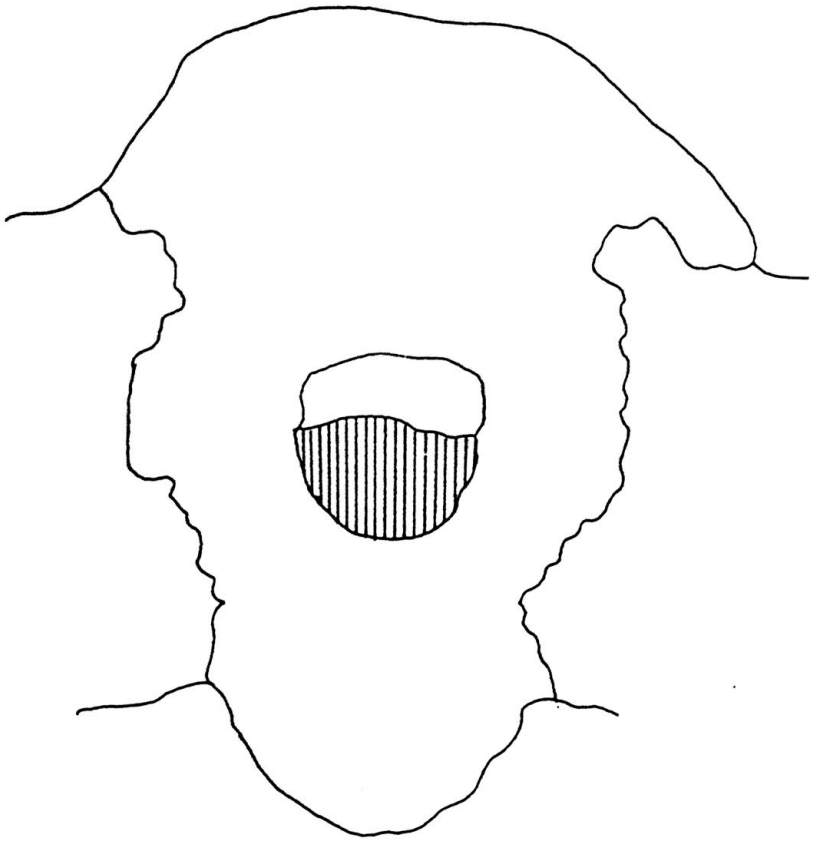

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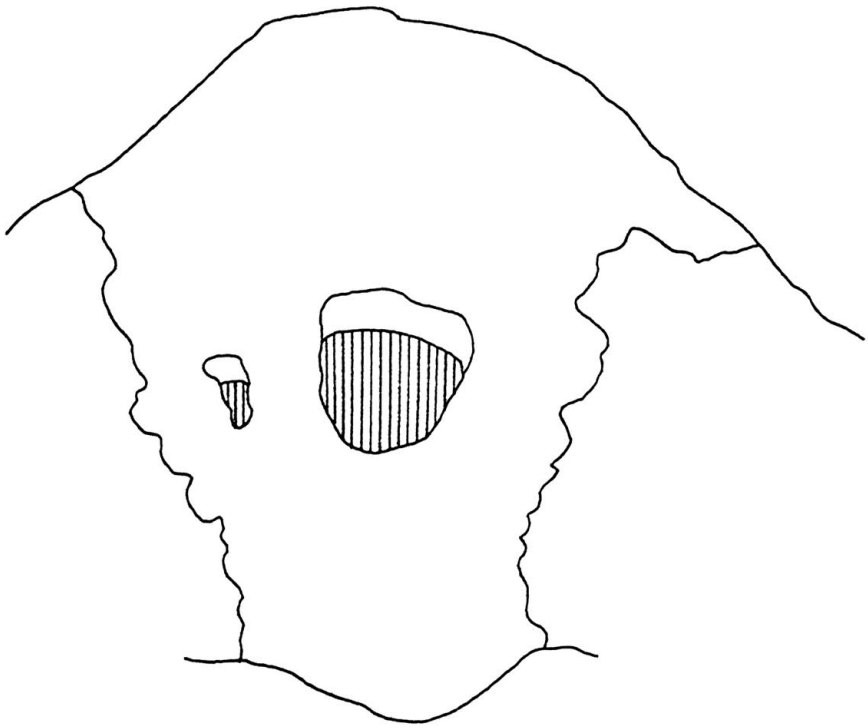

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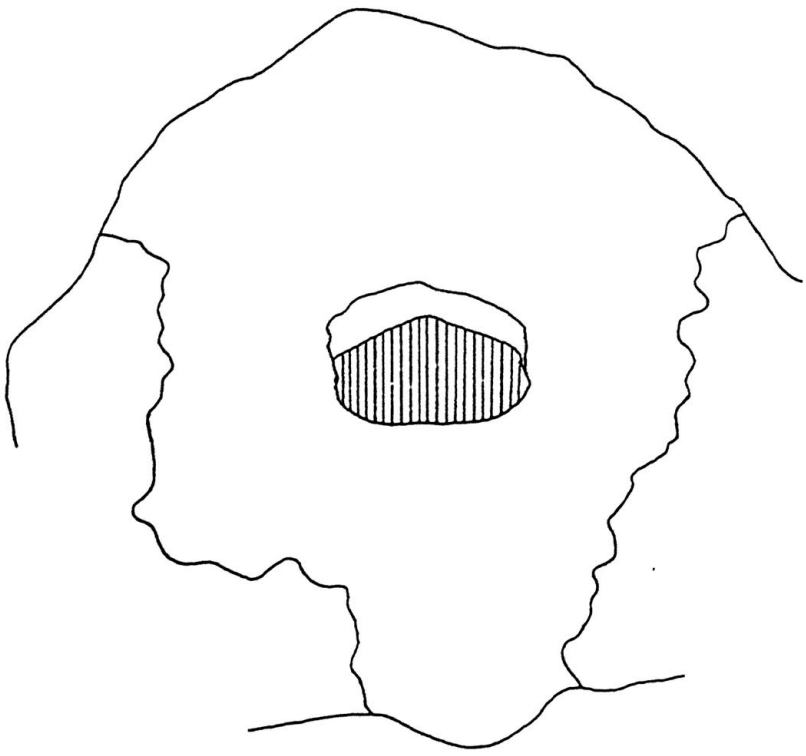


Fig. 24

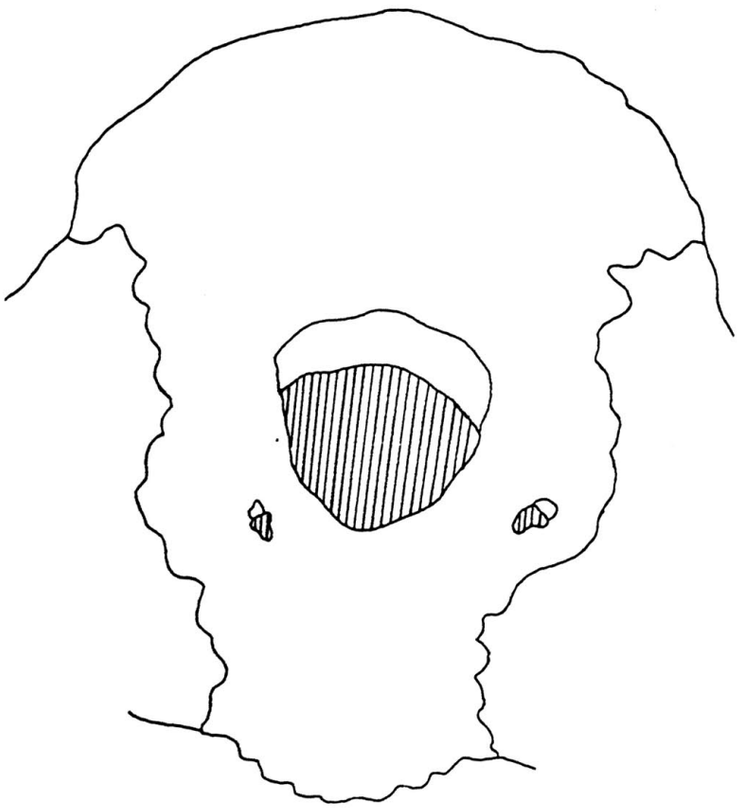
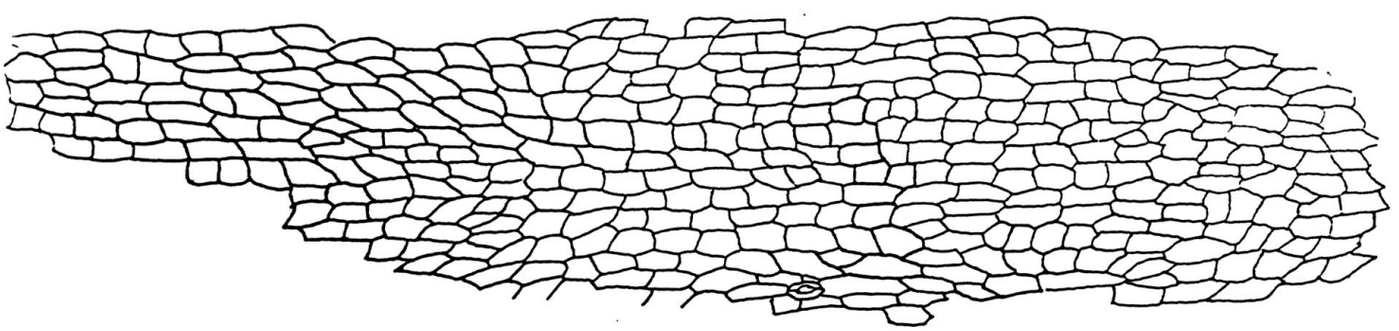


Fig. 25



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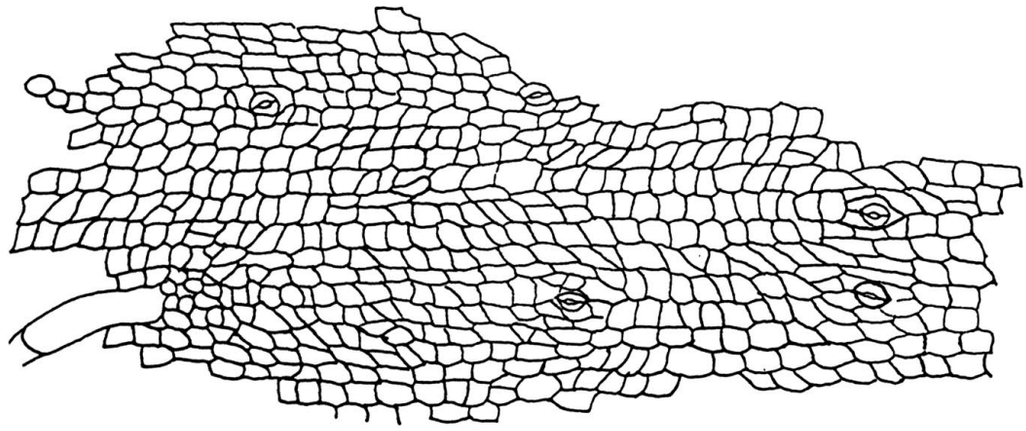
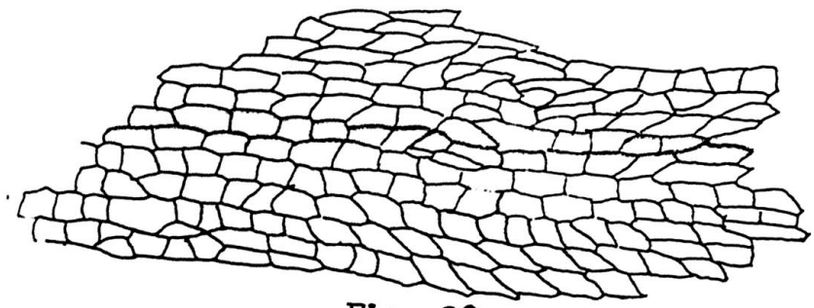


Fig. 27



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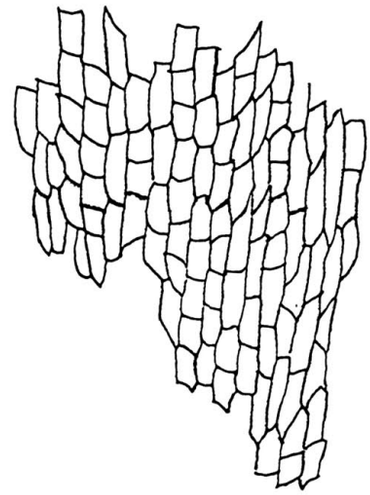

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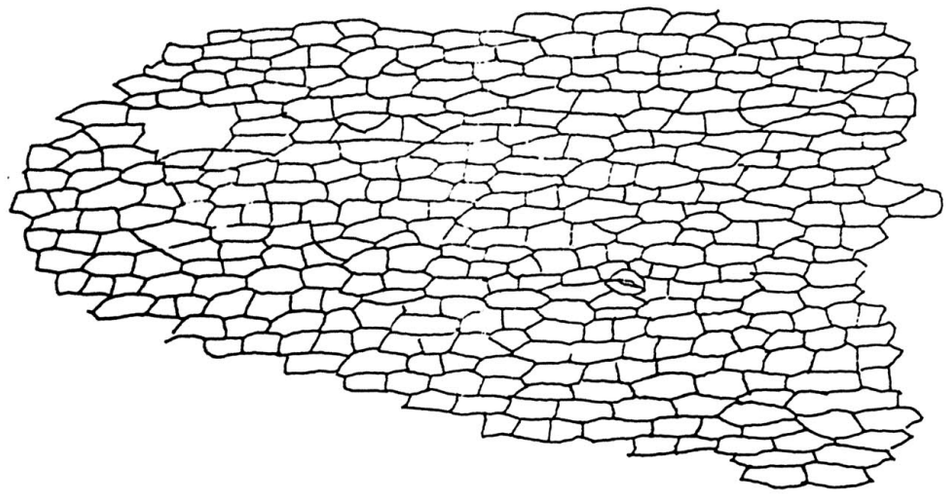

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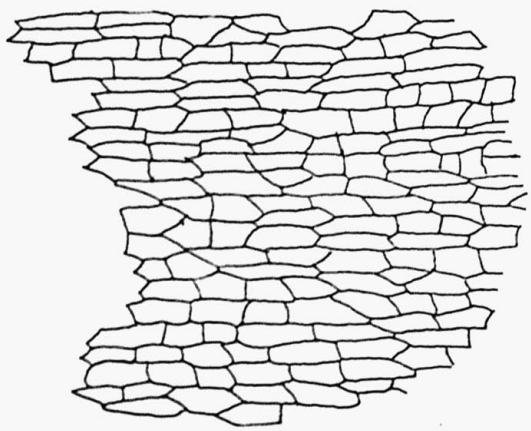

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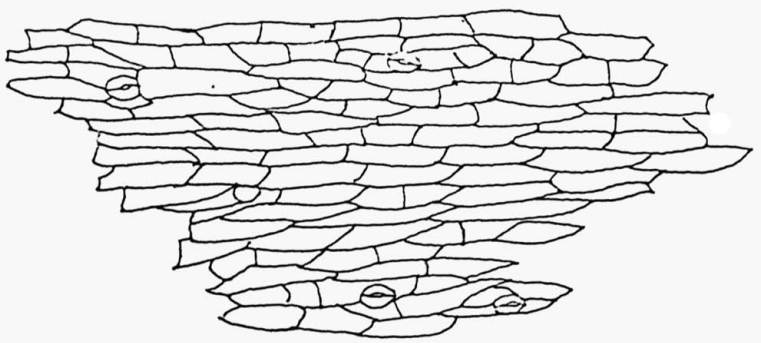

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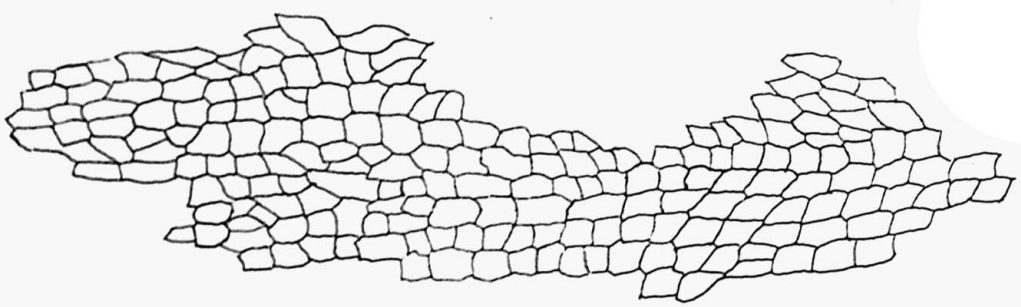


Fig. 33

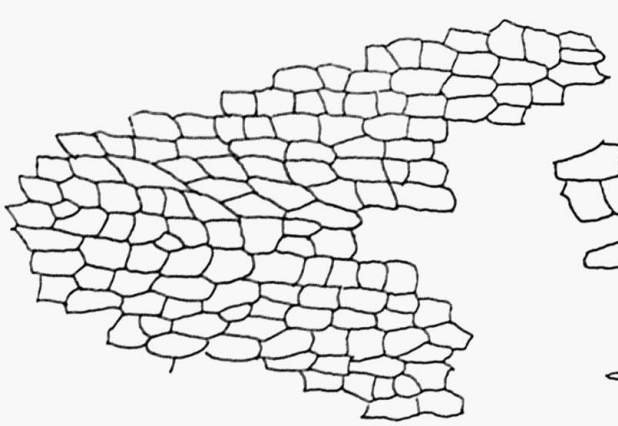


Fig. 34

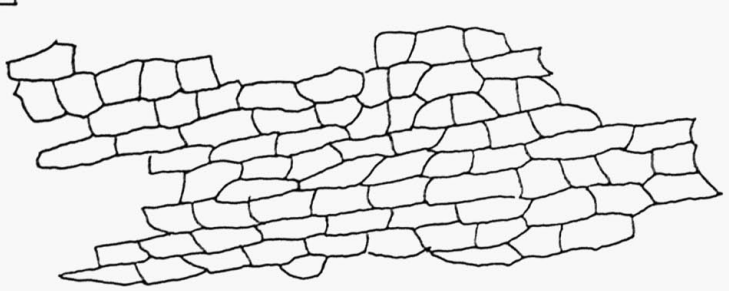


Fig. 35

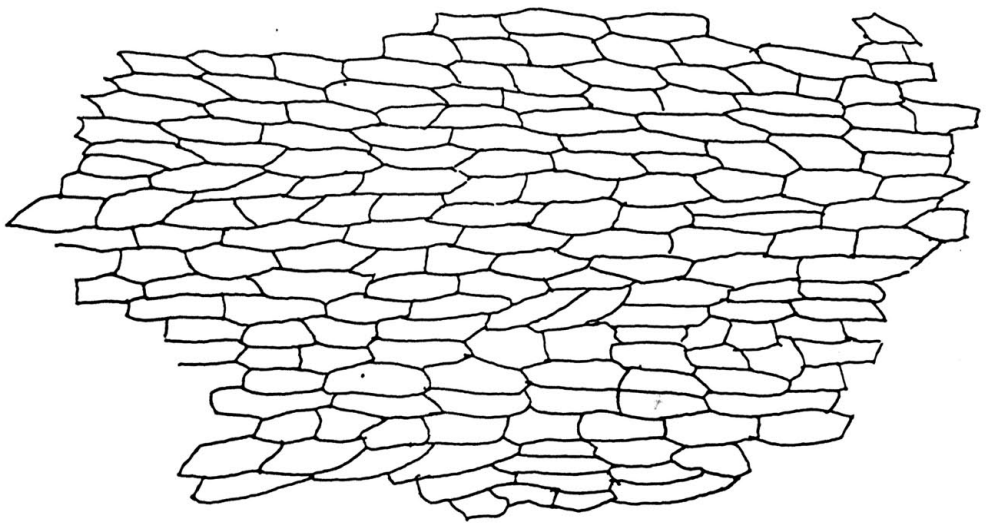


Fig. 36

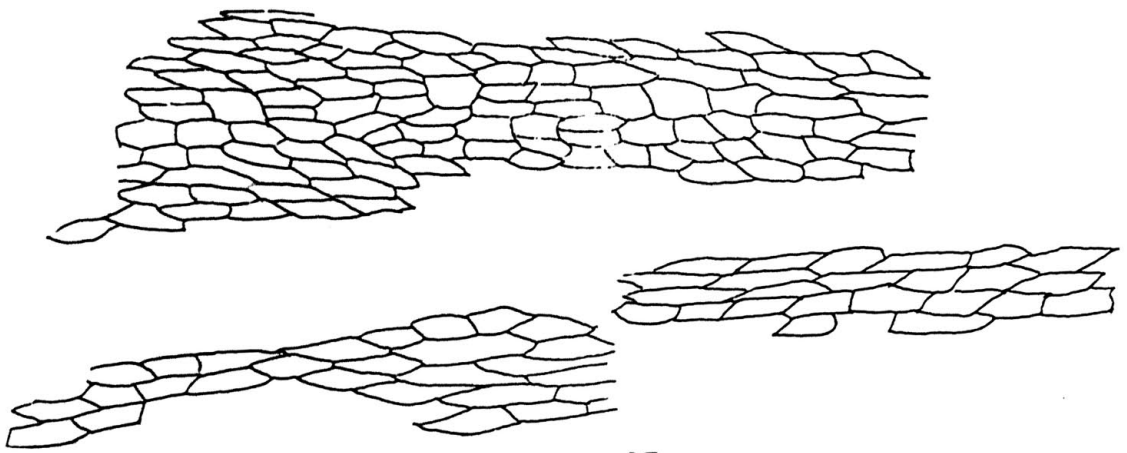


Fig. 37

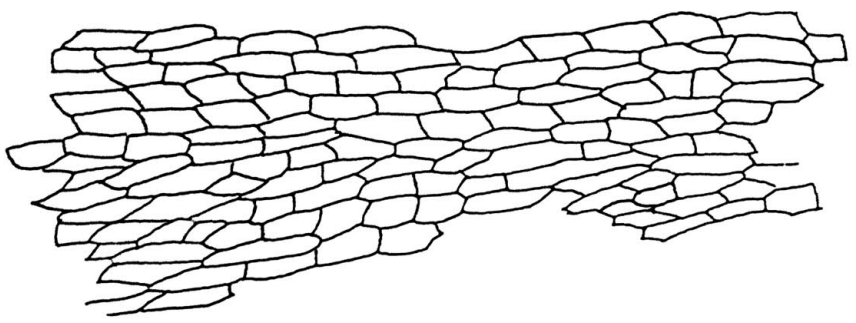


Fig. 38

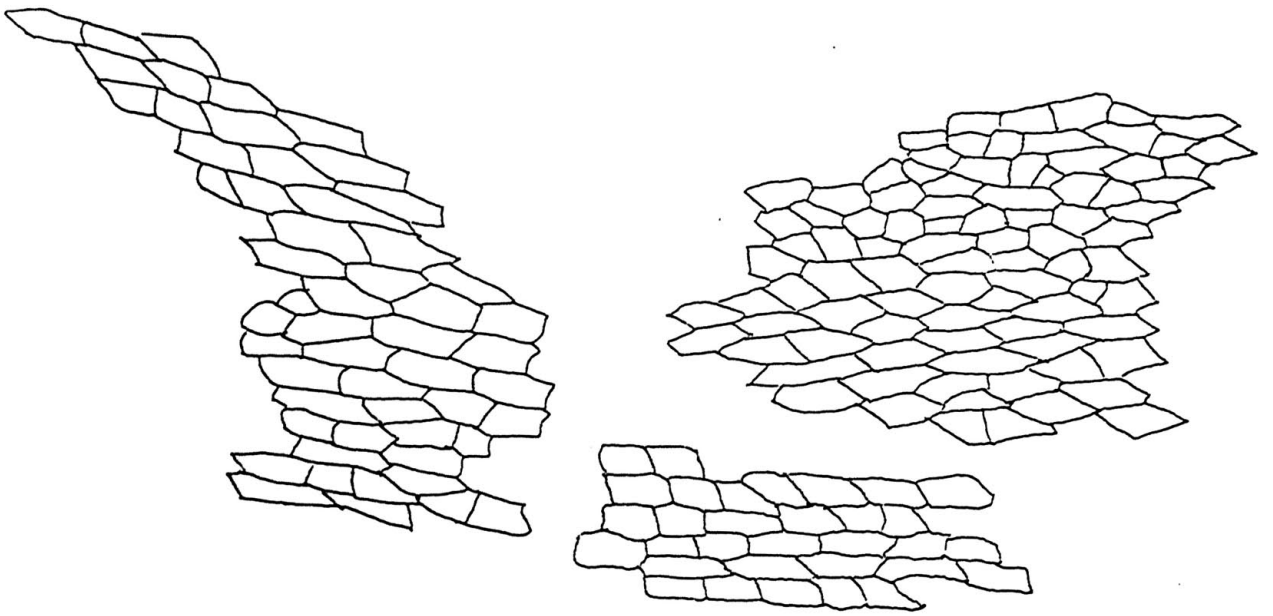


Fig. 39

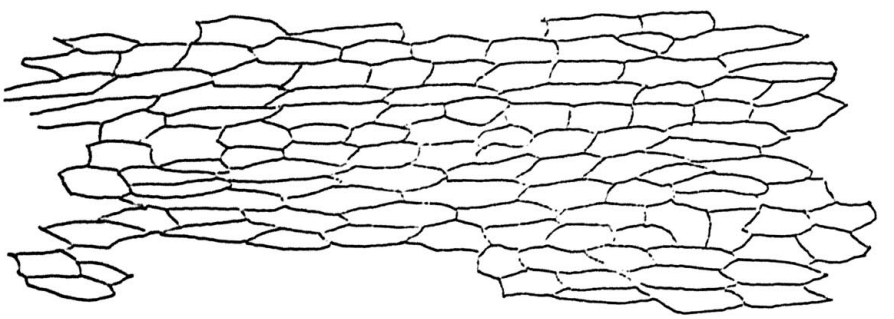
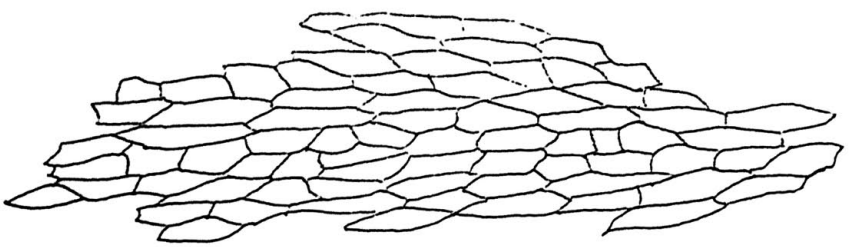


Fig. 40



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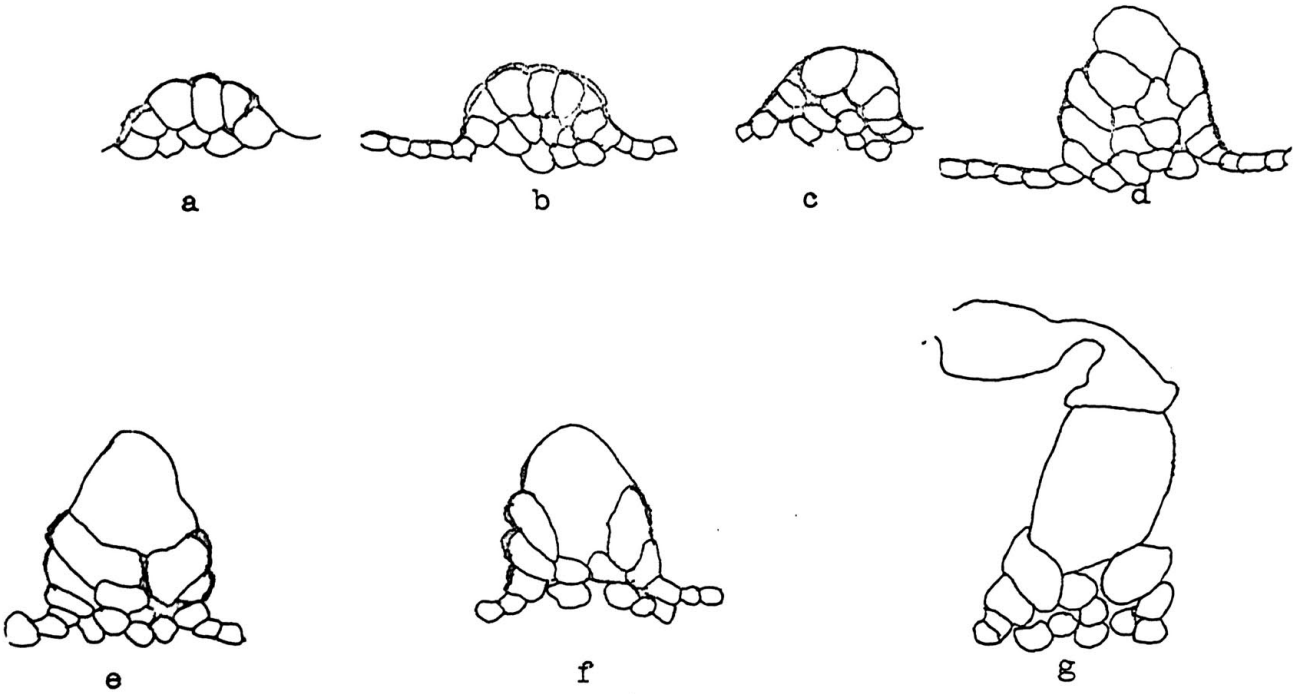


Fig. 42

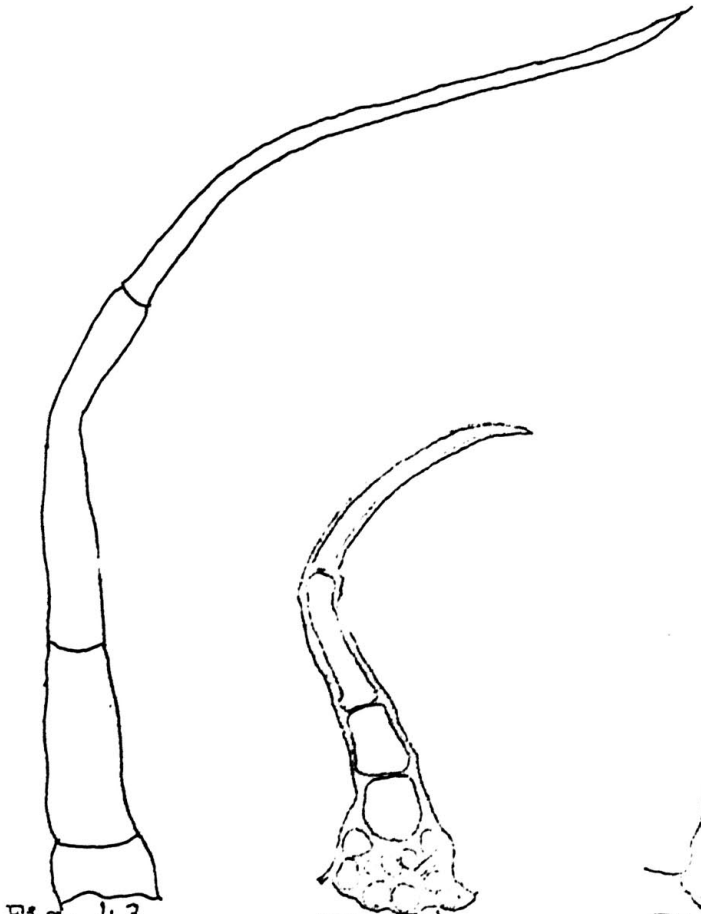


Fig. 43

Fig. 44

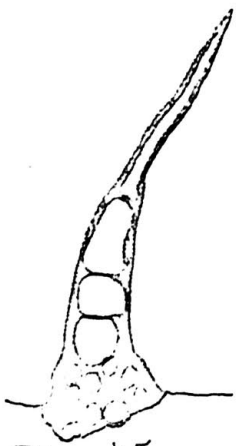


Fig. 45

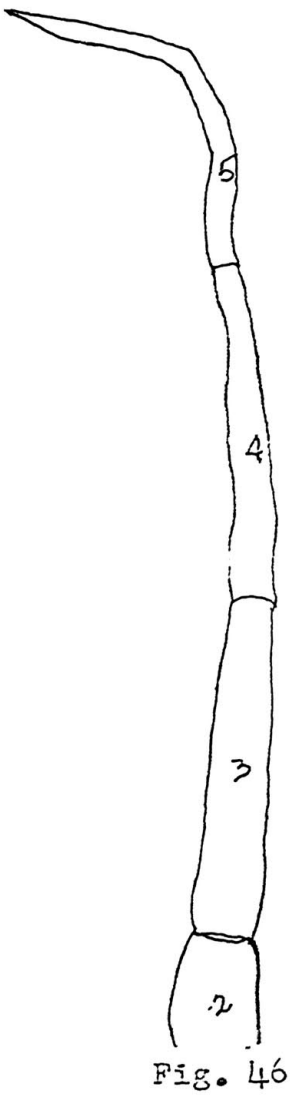
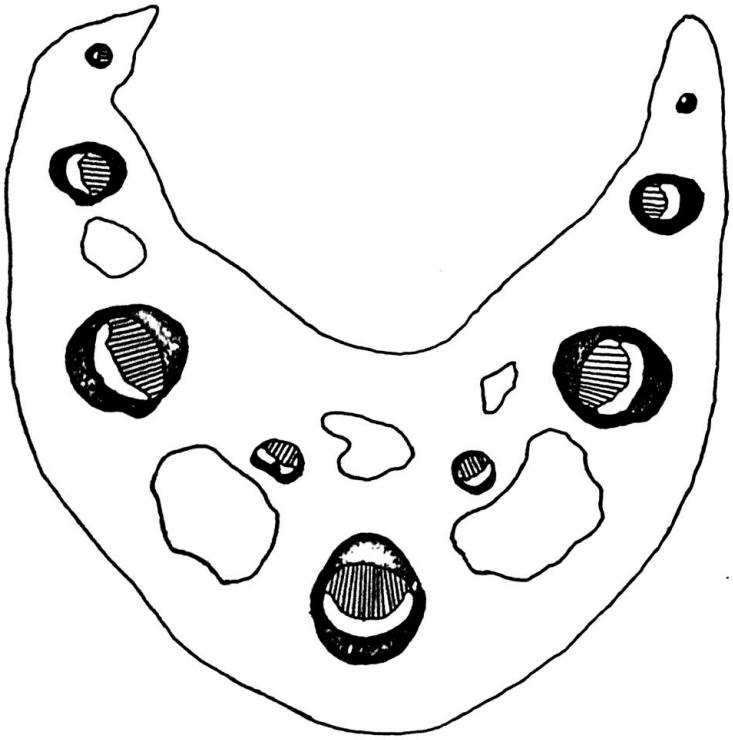


Fig. 46



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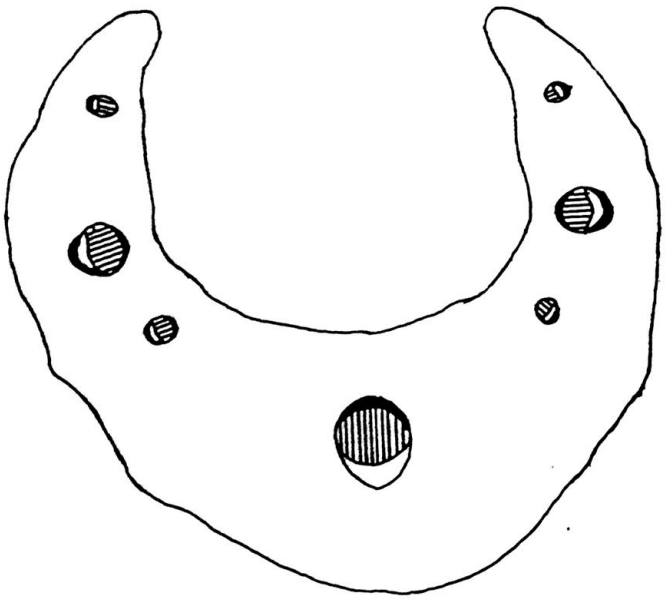


Fig. 48

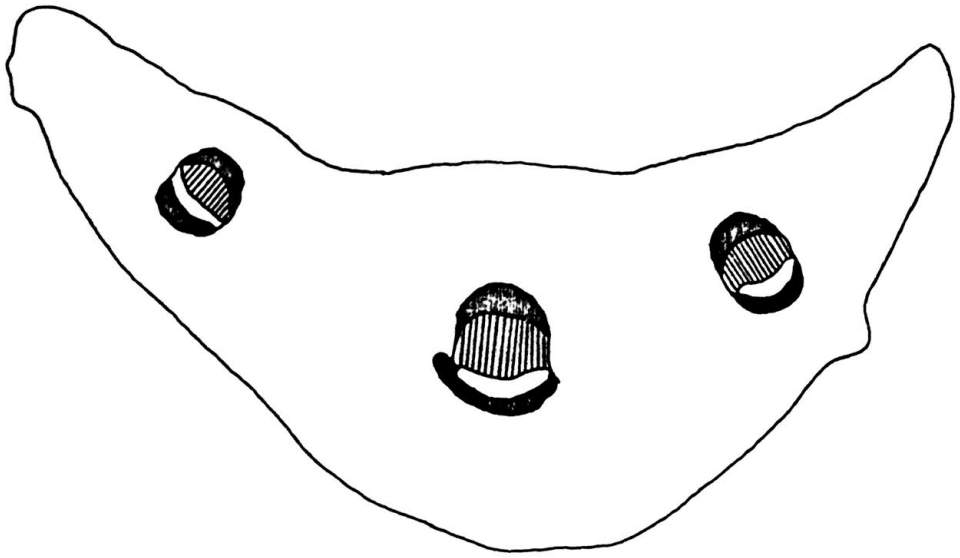


Fig. 49

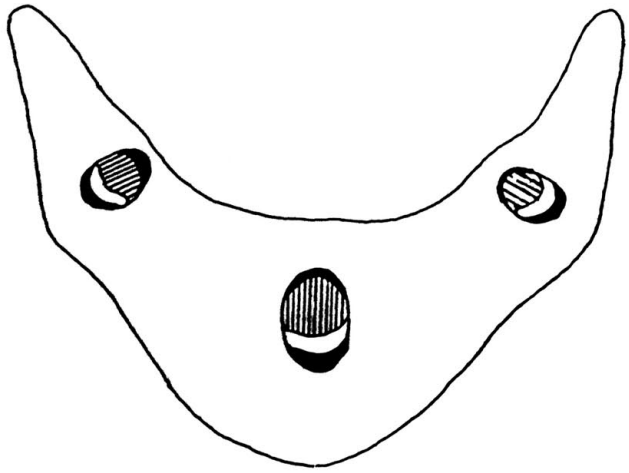


Fig. 50

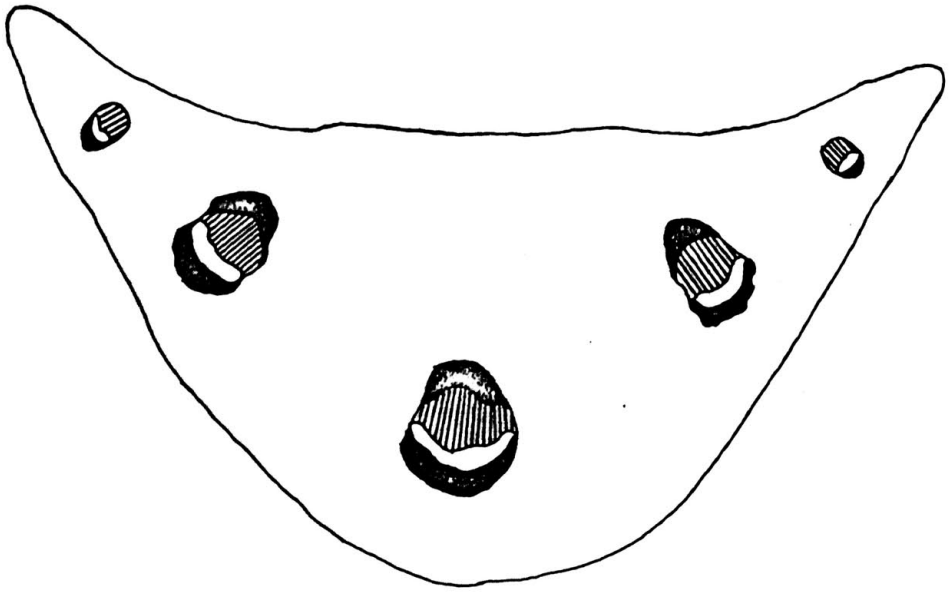


Fig. 51

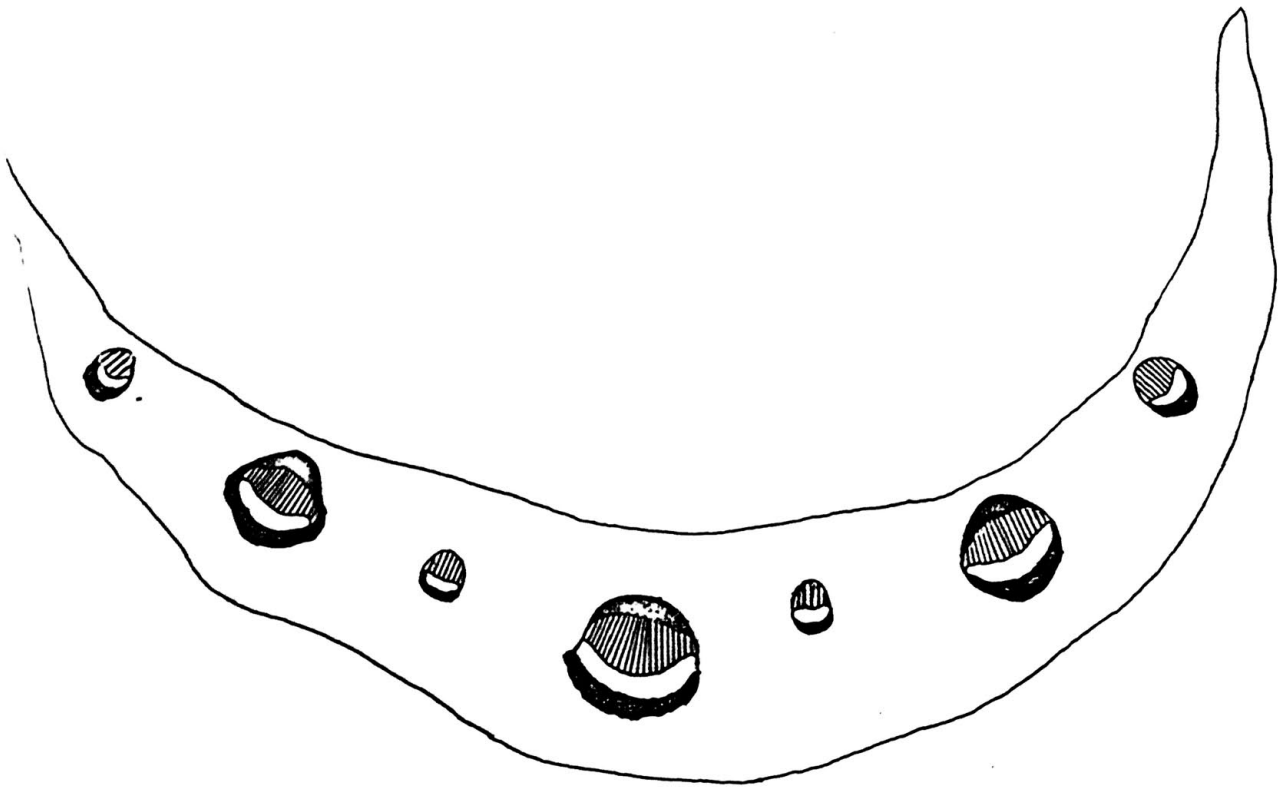


Fig. 52

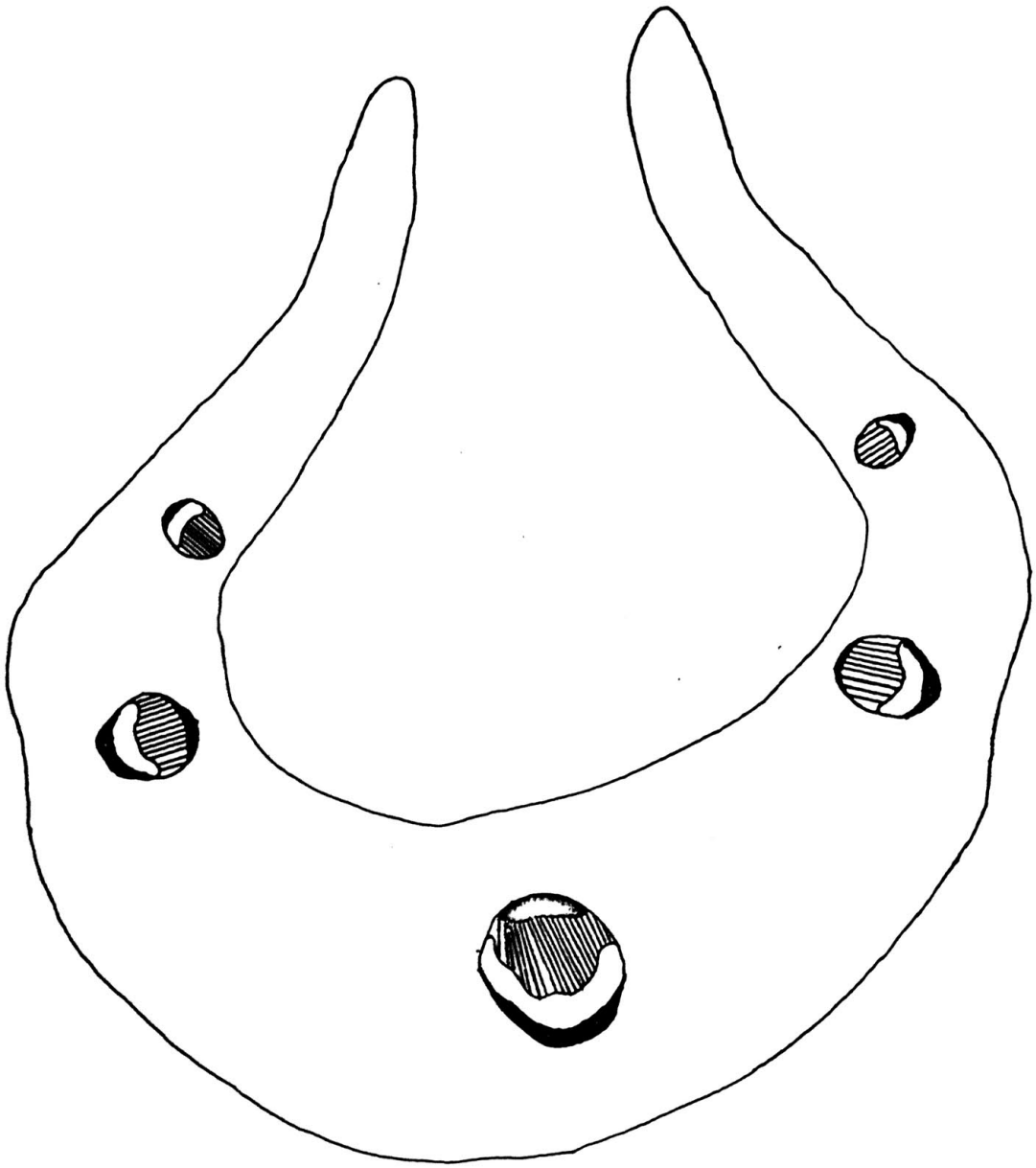


Fig. 53

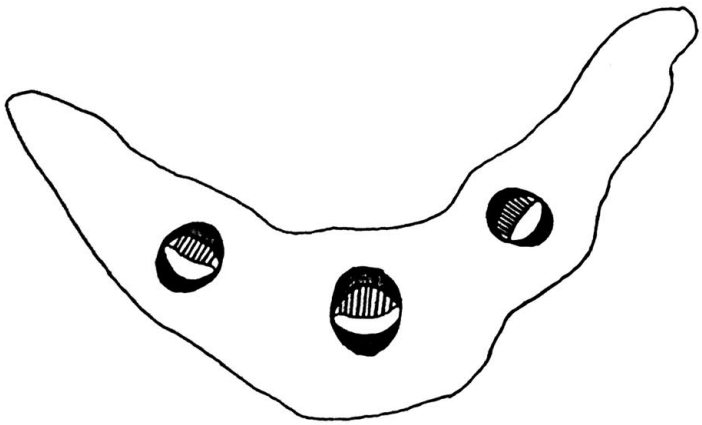


Fig. 54

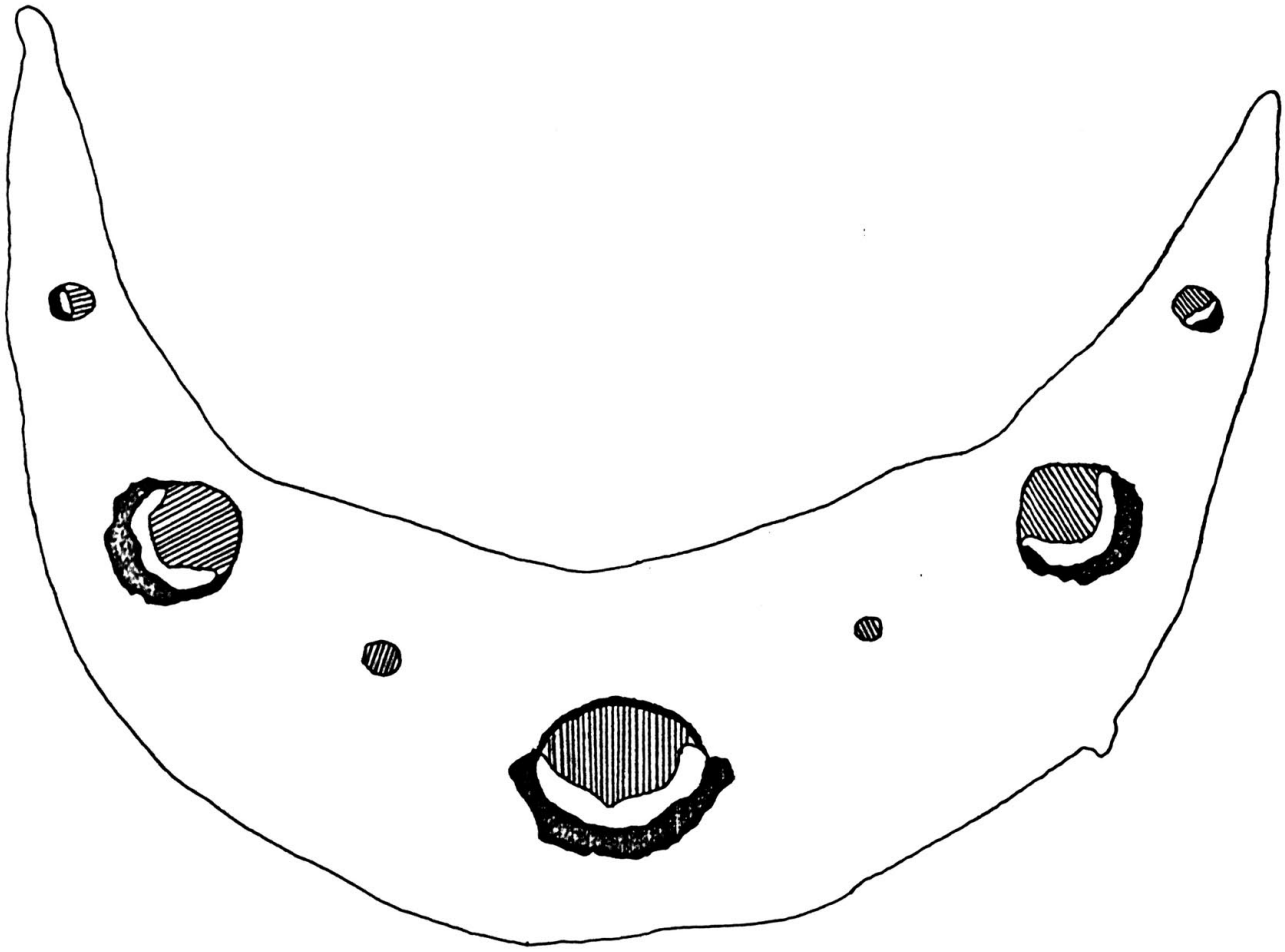


Fig. 55

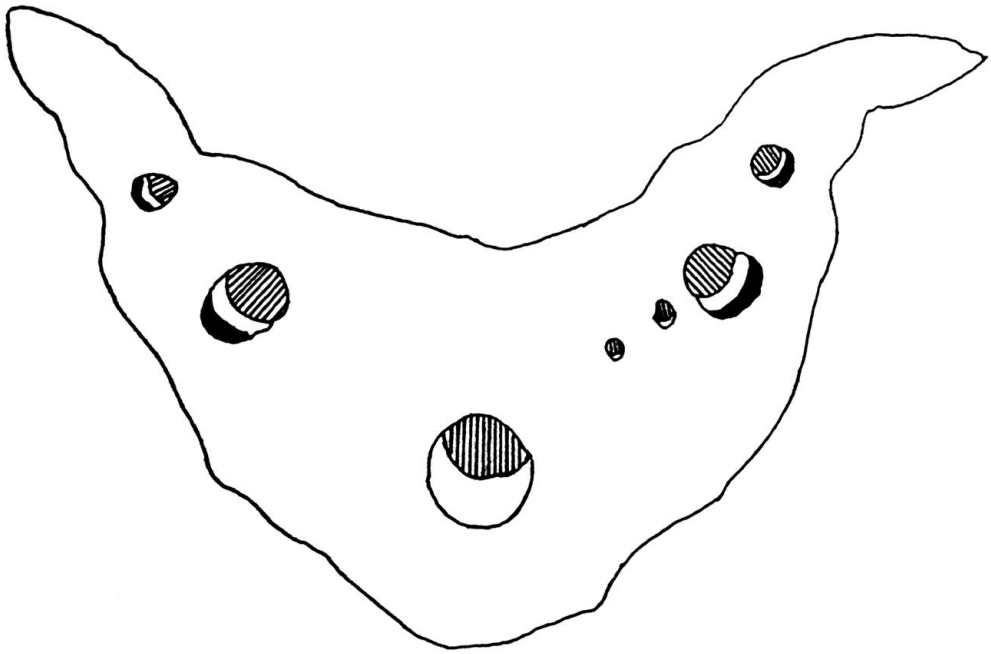


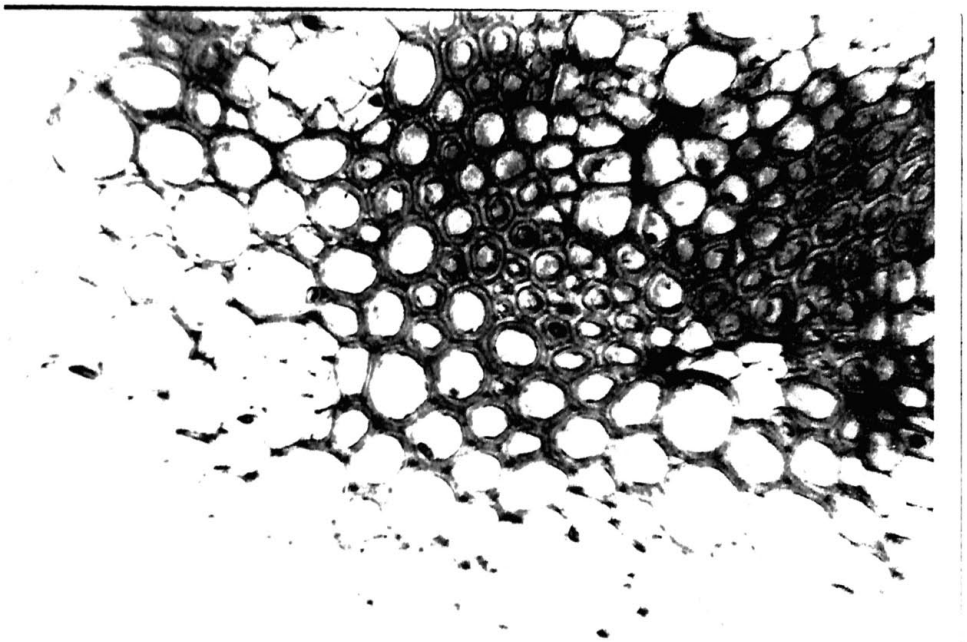
Fig. 56

Fig. 57 (X 430)

From E. paradoxa var. neglecta is shown canals of stem. Often as many as three canals appear in close association with vascular bundles although slight rearrangements situate canals along the sides. Here, one can see two canals opposite the vascular bundles, another along the side.

Fig. 58 (X 430)

Canal of pith shown in transectional view from E. paradoxa var. neglecta demonstrating many celled (12) epithelial ring.



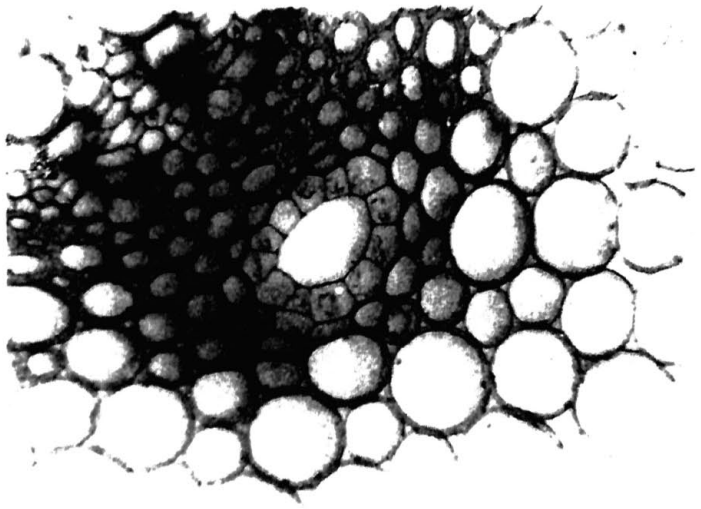
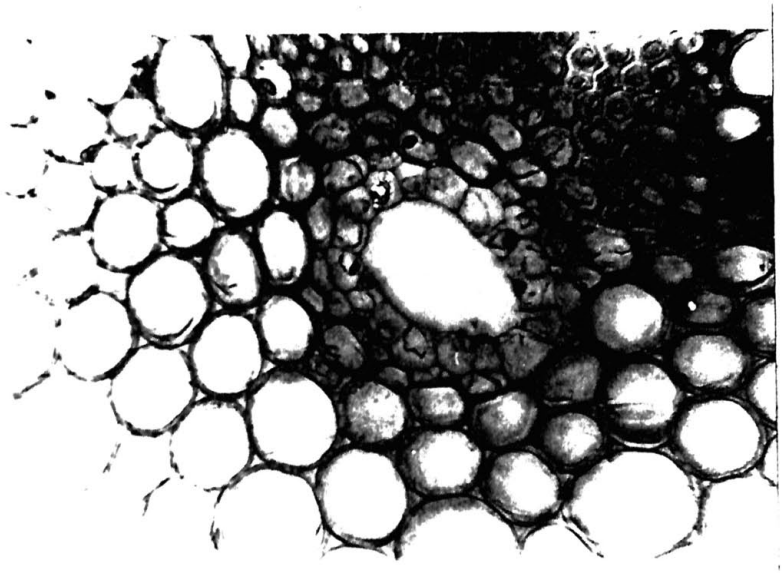


Fig. 59 (X 430)

From E. paradoxa var. neglecta is shown a canal of the stem. Notice the comparatively enormous size of the canal cavity. These canals are located near protoxylem points surrounded by little or no sclerified tissue. This canal is the largest found anywhere in the genus.

Fig. 60 (X 430)

A transectional view from E. speciosa stem. Note paired secretory canals opposite protoxylem points. Many canals of this species are not well-defined due to incomplete development.



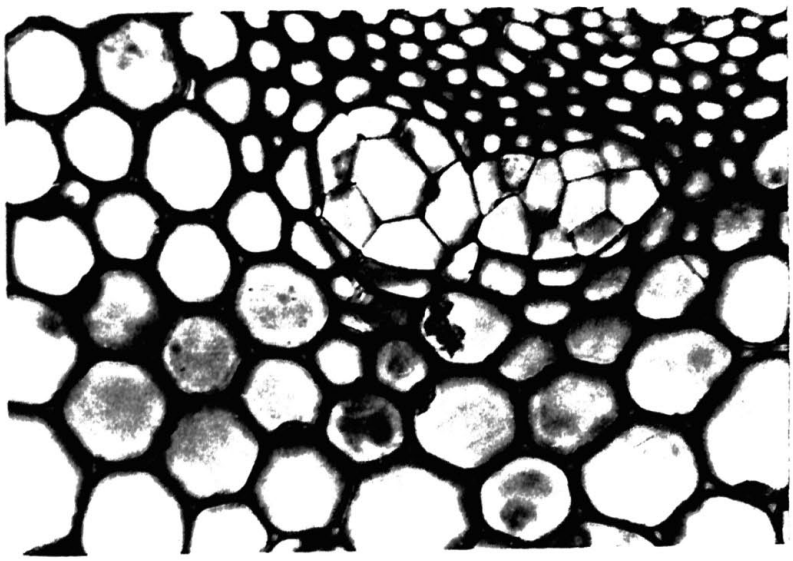
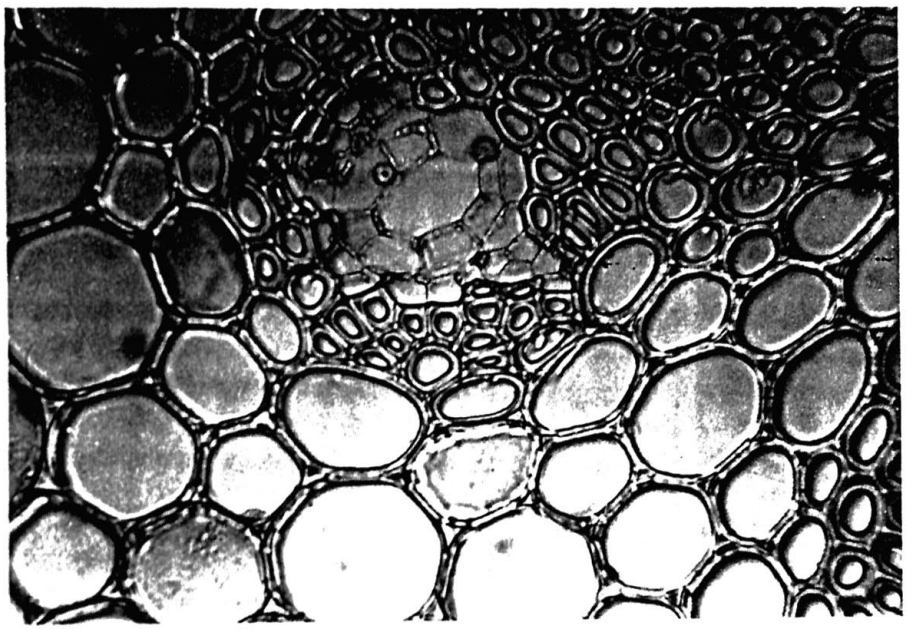


Fig. 61 (X 430)

Shown in transectional view is a canal from the stem of E. atrorubens. The canal shown consists of an eight celled epithelial ring surrounded by thin-walled accessory tissue. Note the rectangular shape of epithelial cells.

Fig. 62 (X 430)

Portion of Fig. 66 showing canal and overunder arrangement of thin-walled accessory tissue. Notice that E. atrorubens has extensive sclerification surrounding canals.



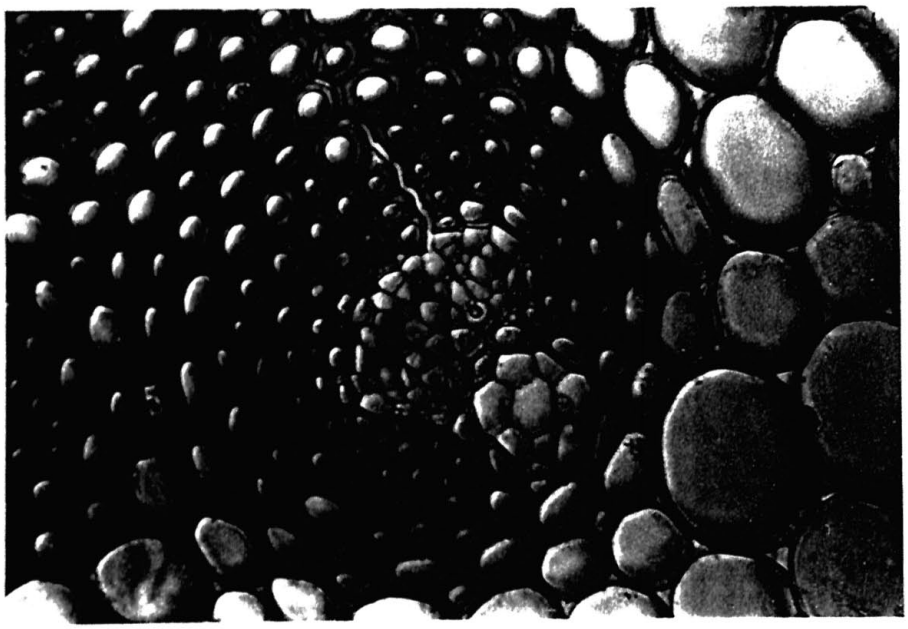


Fig. 63 (X 970)

Shown in transectional view is a sector of the stem from E. pallida. Note secondary growth being initiated in interfascicular region. In the lower right corner a poorly differentiated canal is shown with accompanying thin-walled accessory tissue. Canals appear opposite the interfascicular region. Chlorenchymatous tissue can be seen in the upper left corner.

Fig. 64 (X 430)

Shown in longisectional view is endodermal cell of E. pallida. Note numerous starch grains with rough, ridged surfaces. Starch grains measure approximately 4.6 μ in cross diameter.

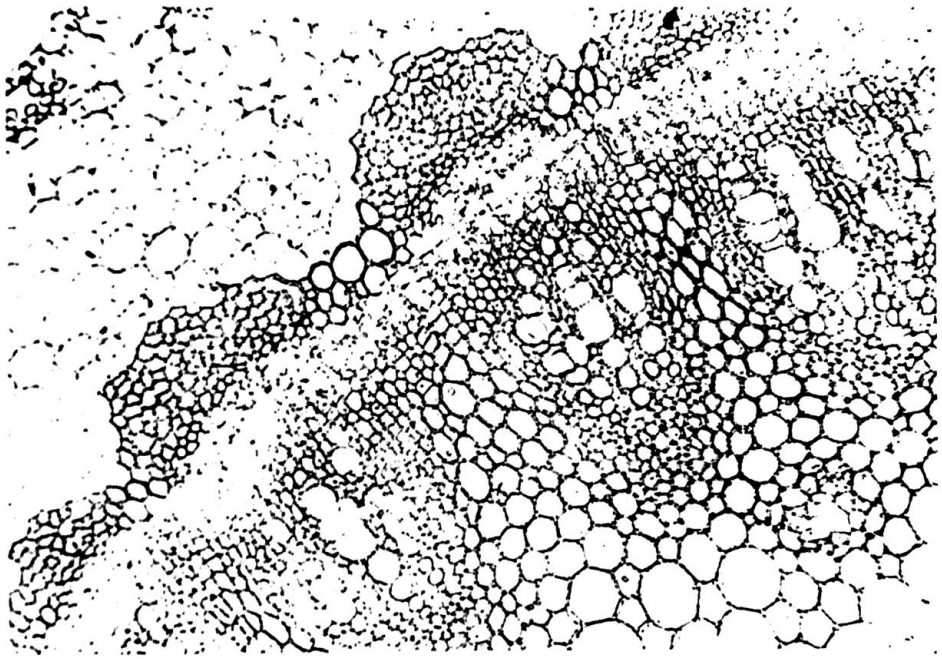
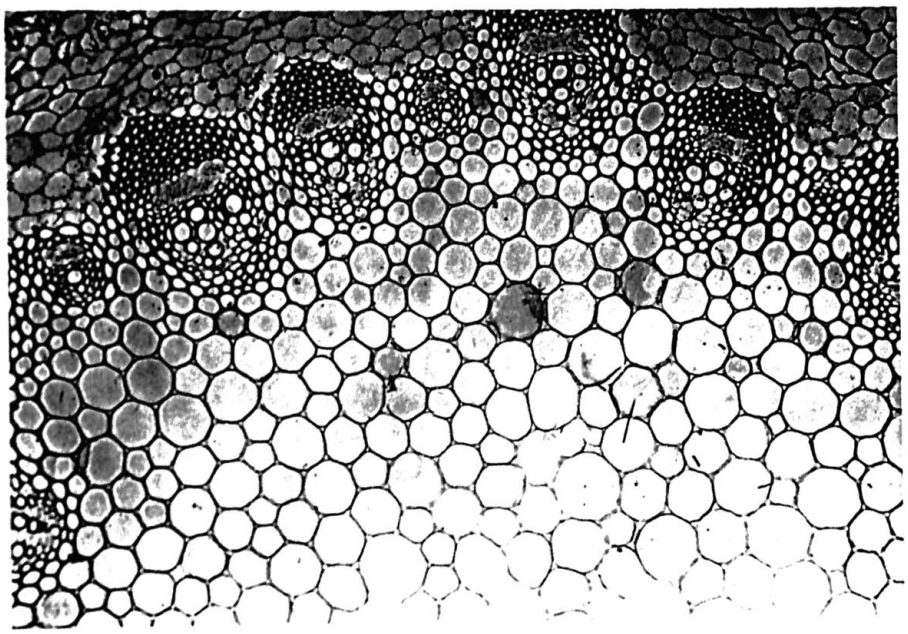


Fig. 65 (X 100)

Shown in transectional view is the stem from E. sanguinea. Note the absence of canals in the pith. Of special interest is the wholly parenchymatous pith. Interfascicular regions have become sclerified modifying wall thickness of essentially parenchymatous tissue. The section was prepared by using tertiary butyl alcohol, microtomed at 10 μ , and stained with safranin-fast green.

Fig. 66 (X 100)

Shown in transectional view is the stem from E. atrorubens. The section was prepared by the free hand sectioning method and stained with safranin-fast green. Note pith canals opposite protoxylem points accompanied by variable amounts of thin-walled accessory tissue. Opposite the interfascicular region occurs one cortical canal. In the lower left foreground a canal is shown adjacent to the endodermis.



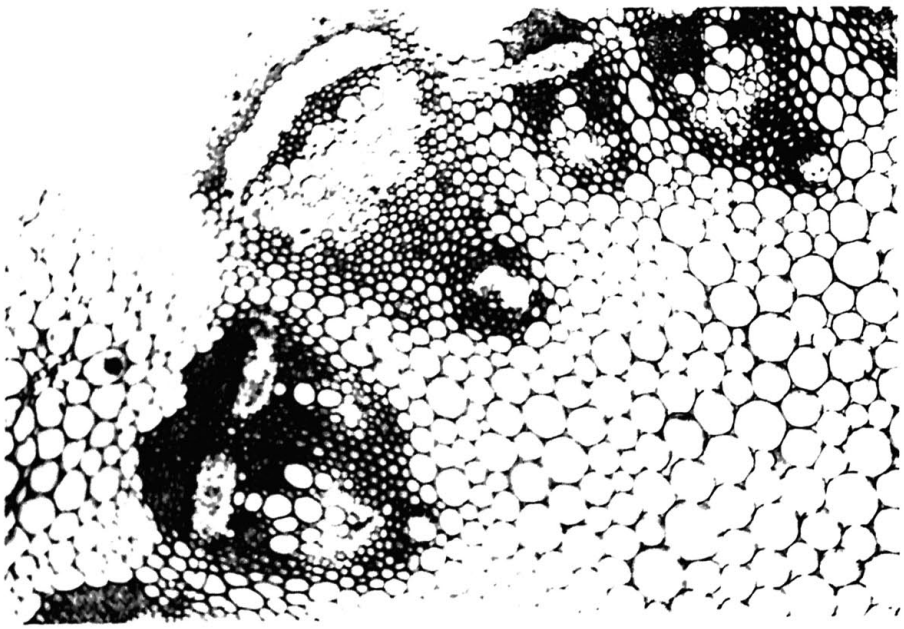
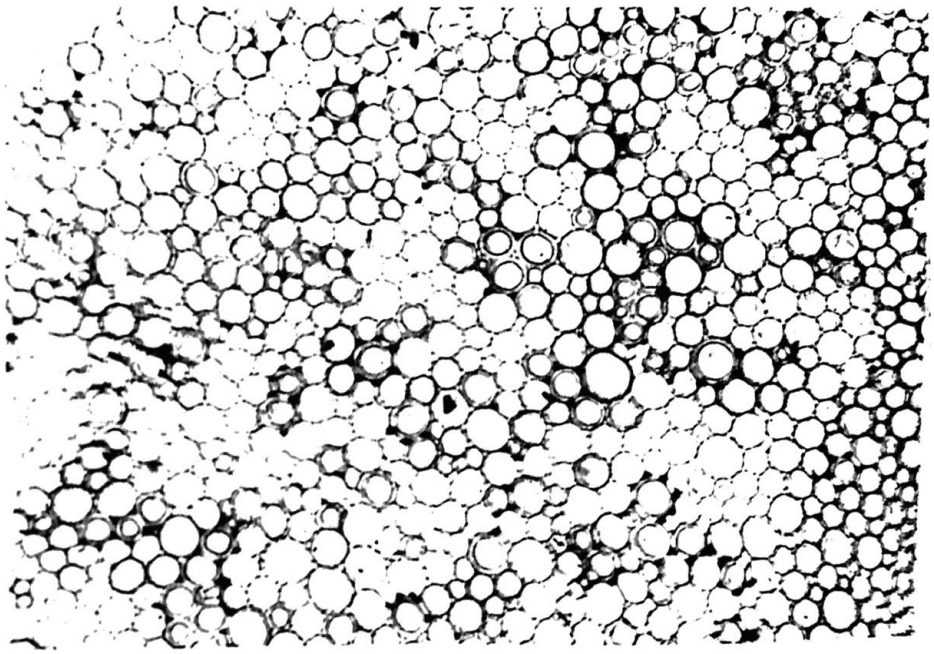


Fig. 67 (X 400)

Shown in transectional view is the pith from E. angustifolia var. angustifolia race intermedia stem. Sclerosis of the pith is a progressive phenomena; here, only partial sclerification can be seen. Sclerotic cells have thick secondary walls with a black substance filling intercellular spaces.

Fig. 68 (X 430)

Transectional view from E. angustifolia var. angustifolia stem. Greater magnification shows the nature of thick walled pith cells.



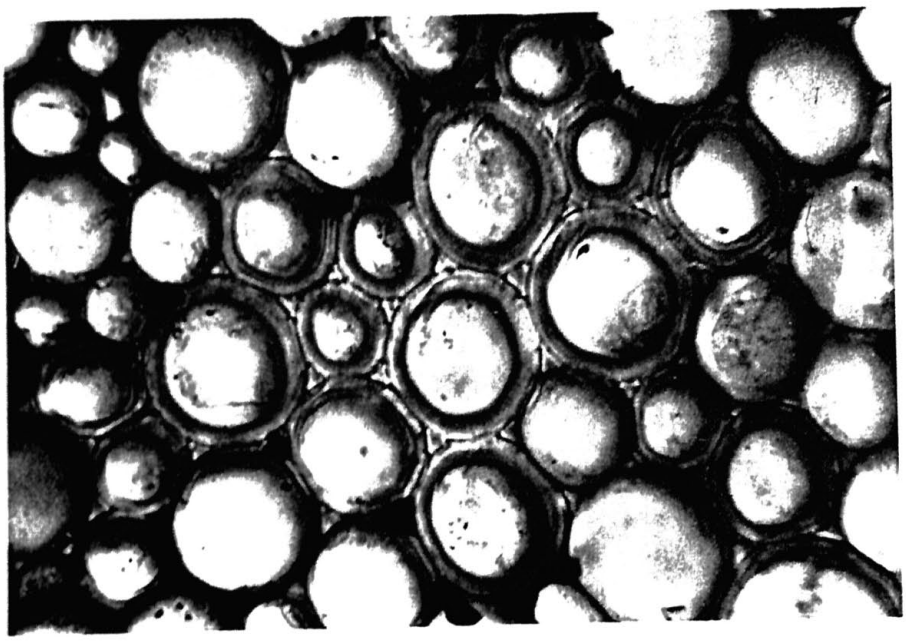
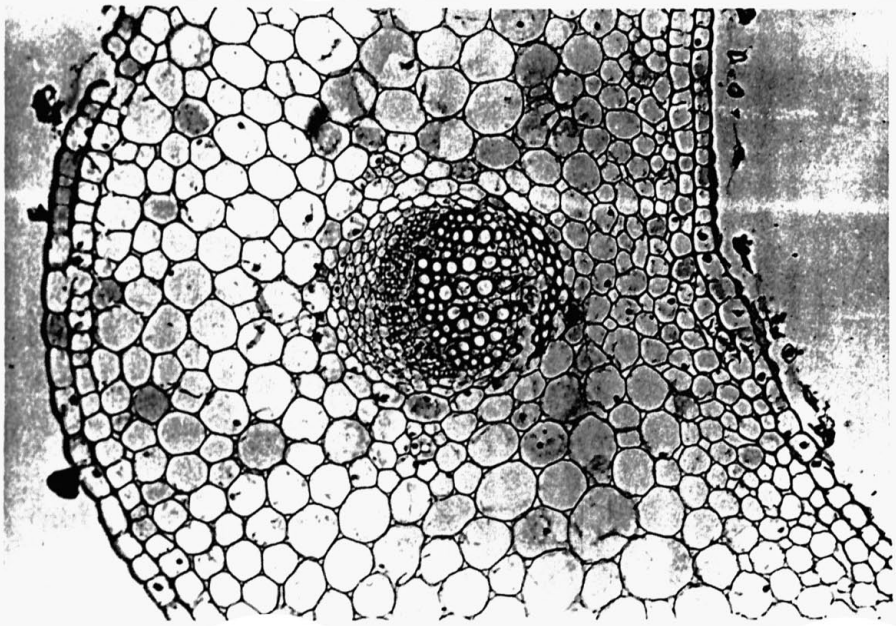


Fig. 70 (X 100)

A transectional view of E. sanguinea petiole showing medial vascular bundle without abaxial fibrous cap. Two small canals (30.0\μ) are located on each side of the medial vascular bundle.

Fig. 69 (X 35)

Shown in transectional view is a petiole of E. atrorubens. Note the large lacunae positioned around the medial vascular bundle. Each vascular bundle is completely ensheathed by fibrous tissue.



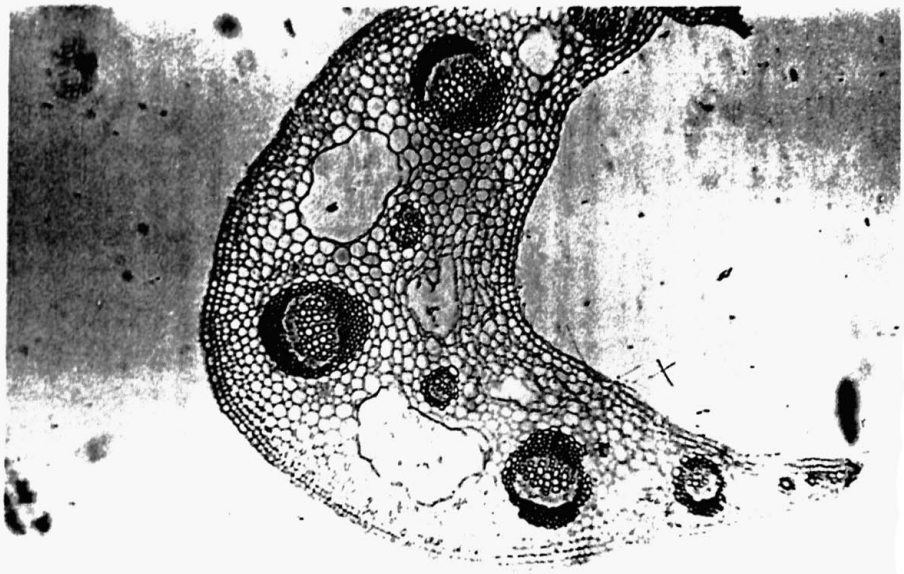
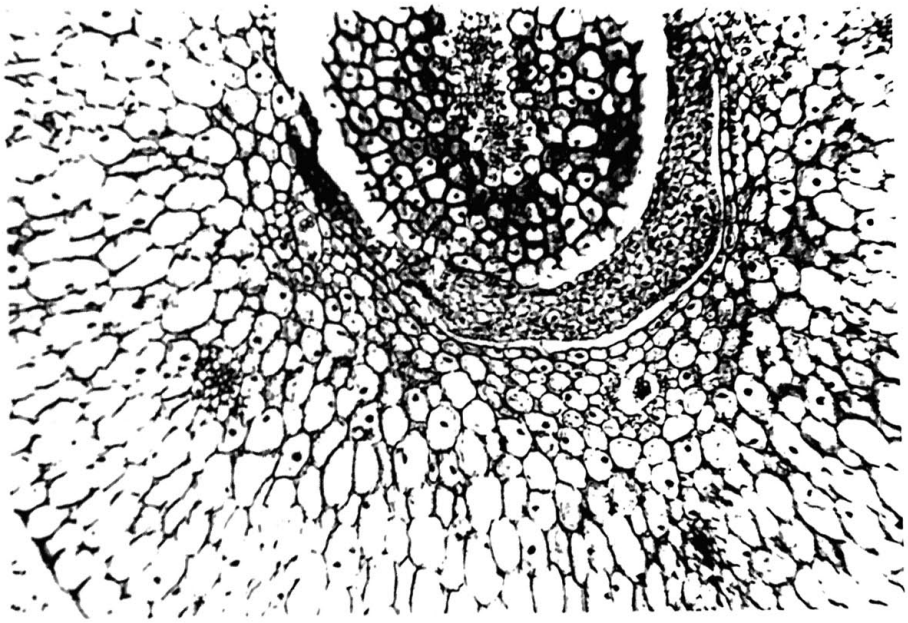


Fig. 71 (X 100)

Shown in transectional view is a disc floret of E. atrorubens. Of special interest in Echinacea is a cup-shaped structure into which the style is inserted just above the ovary. This section passes through the style, cup-structure, fleshy corolla wall, and, not shown, membranous pappus. Note that sclerotic tissue is absent. In left corner can be seen a tiny part of pappus.

Fig. 72 (X 100)

Shown in transectional view is a disc floret of E. atrorubens. Note the style, five filaments, and surrounding corolla tube.



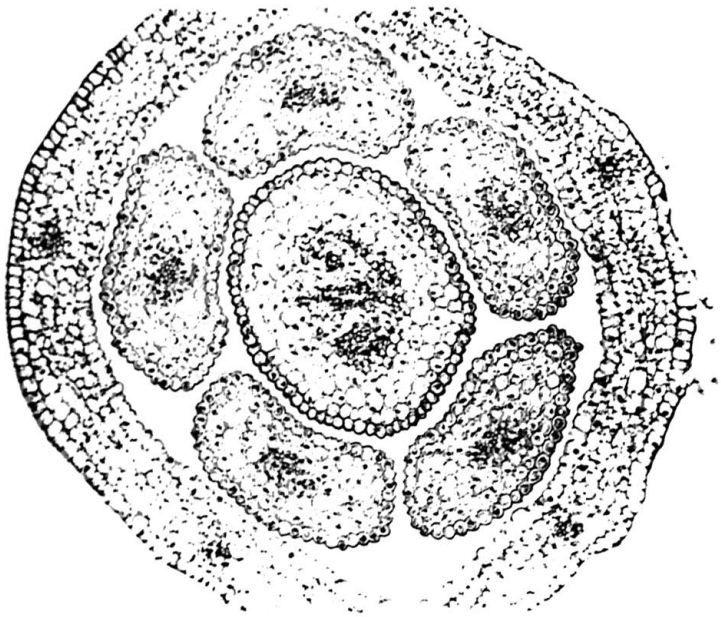
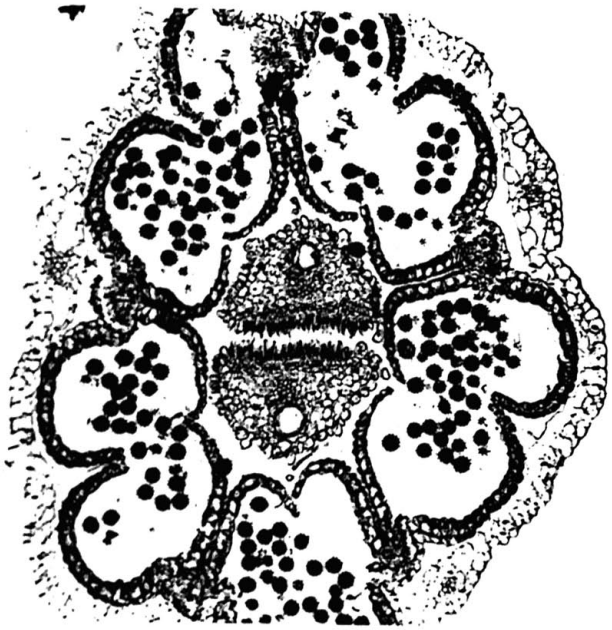


Fig. 73 (X 100)

Shown in transectional view is a disc floret of E. atrorubens. Note the five bilocular, united anthers surrounding the two-parted style. The gamopetalous corolla encloses the reproductive structures.

Fig. 74 (X 100)

Shown in transectional view is a disc floret of E. sanguinea. Sections at the base of the floret revealed a double row of sclerotic cells. Nowhere in serial sections of (Fig. 71, 72, 73) can sclerotic tissue be seen. Not shown is part of pappus membrane, that too, consists of sclerotic tissue.



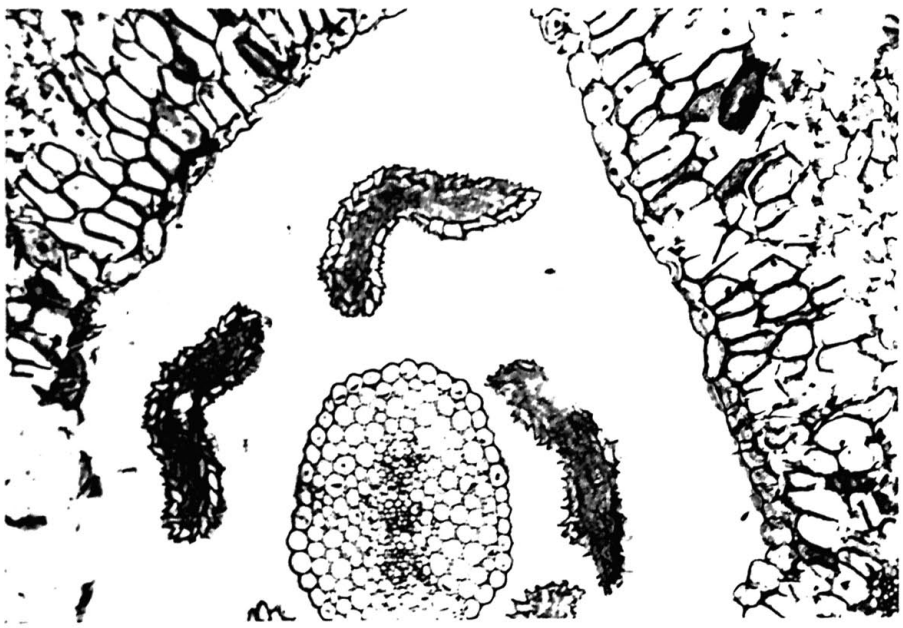
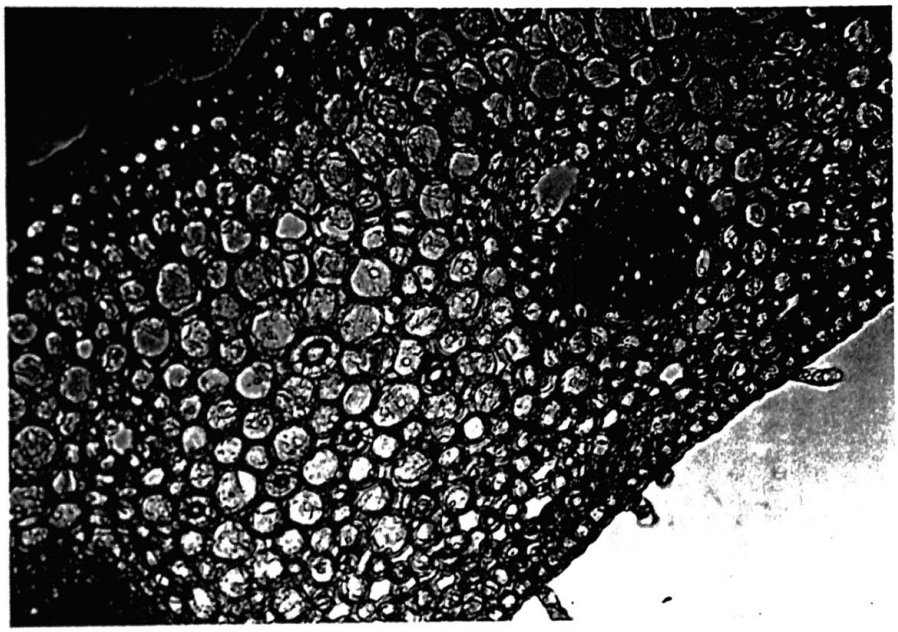


Fig. 75 (X 100)

Shown in transectional view is a petiole from E. paradoxa var. neglecta. Note stone cells scattered throughout fundamental tissue. A relatively large (80.0 μ) canal is situated on the abaxial side of a lateral vascular bundle. Another canal can be seen slightly removed from the medial vascular bundle. These canals can easily be recognized by their large interior cavity. An epithelial ring consists of 5 tc 15 cells.

Fig. 76 (X 430)

Shown in transverse section is the stem of E. angustifolia var. strigosa. A greater part of the cortex is made up of collenchyma in this species. This photomicrograph demonstrates tubular collenchyma found throughout the genus. A cortical canal slightly out of focus is located along the left hand margin.



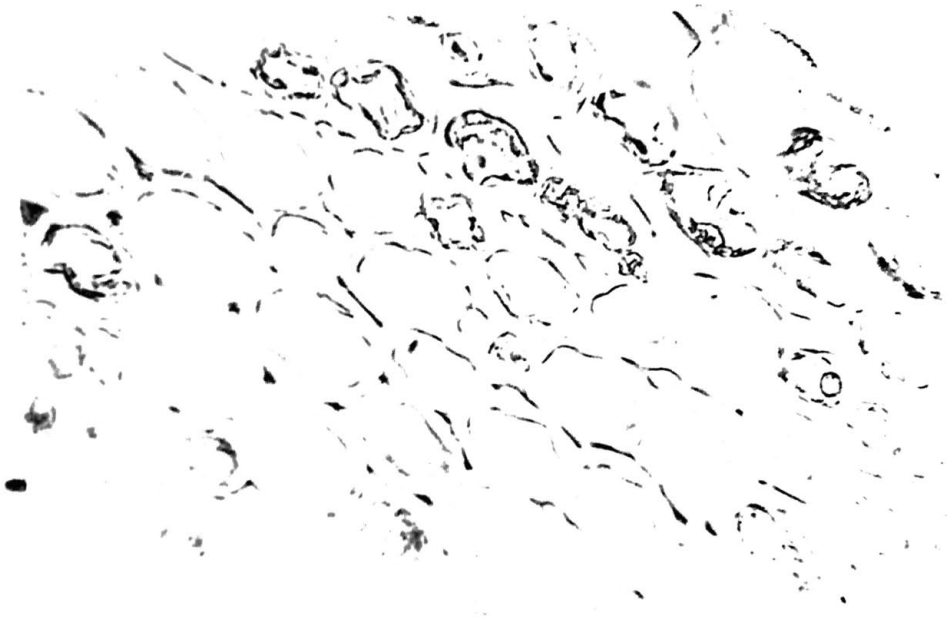
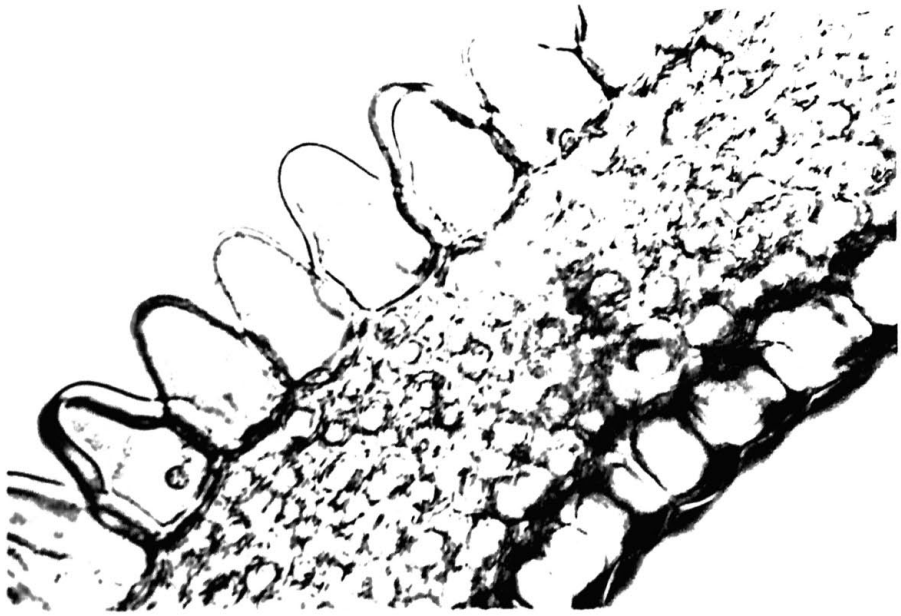


Fig. 77 (X 430)

Shown in transectional view is a ray of E. angustifolia var. angustifolia. Note the nearly bullet-shaped adaxial epidermal cells becoming pinched in part way up outer tangential wall.

Fig. 78 (X 430)

Shown from E. sanguinea is a transectional view of a ray. Note the necked adaxial epidermal cells. An excellent diagnostic character for this species due to the uniformity of the elongate neck.



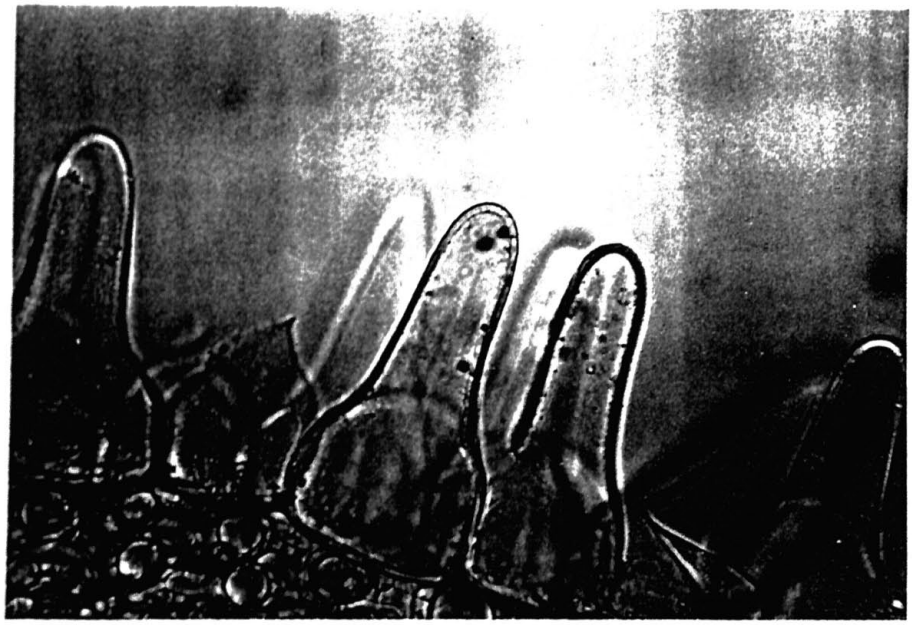
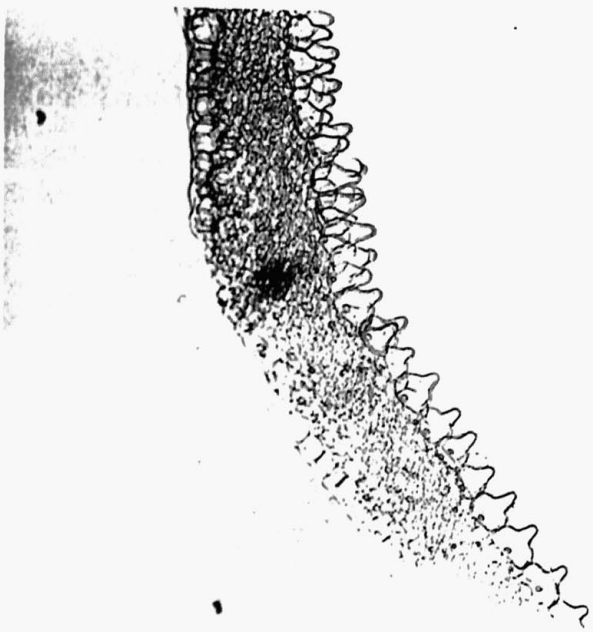


Fig. 79 (X 100)

Shown in transectional view is a ray from E. atrorubens. Cells in the lower foreground demonstrate the papillose condition in adaxial epidermal cells. Some of these cells are very broad as if to give a flattened appearance. Note variability in adaxial epidermal shape shown in upper part of photomicrograph.

Fig. 80 (X 430)

A portion of Fig. 79 taken under greater magnification.



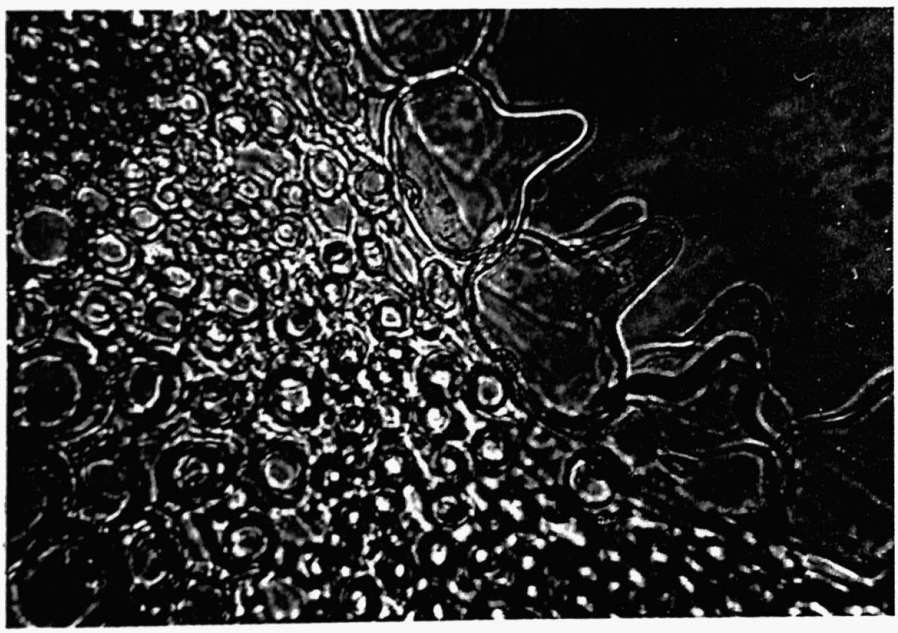
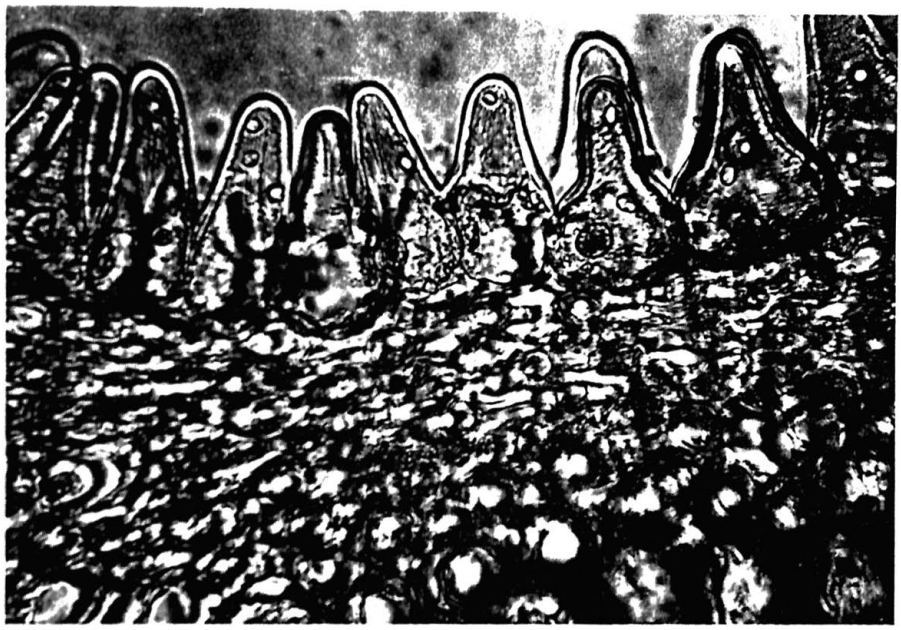


Fig. 81 (X 430)

A transectional view of E. purpurea ray showing adaxial epidermal cells.

Fig. 82 (X 430)

E. angustifolia var. strigosa ray shown in transectional view. Note the lattice-work arrangement of the mesophyll tissue. Compare the size change in armed cells adaxially situated to those adaxial. The air spaces between cells justifies the descriptive term lacunose tissue.



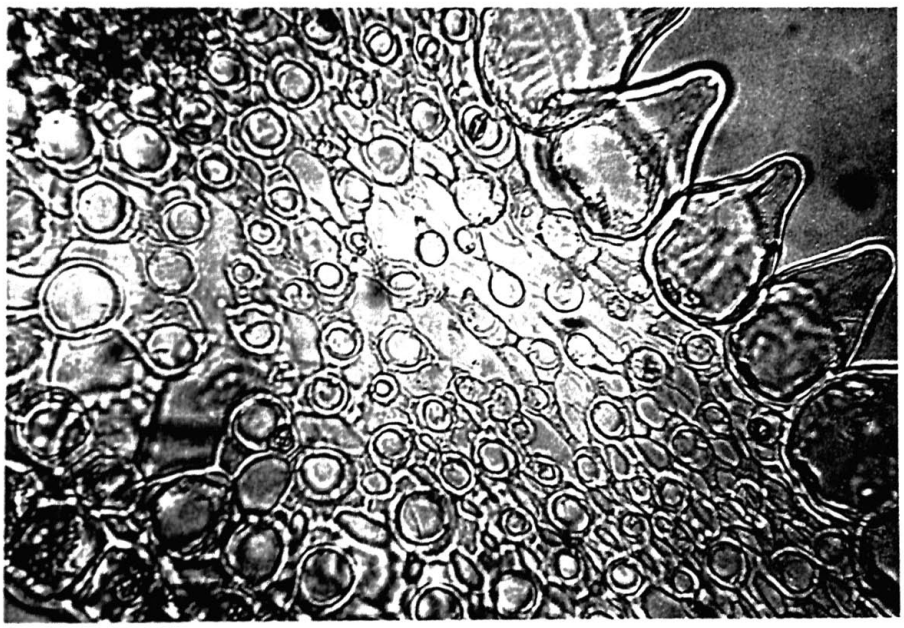


Fig. 83 (X 430)

A transectional view from E. angustifolia var. angustifolia race intermedia ray. Notice the highly magnified adaxial epidermal cells showing an enlarged bulbous basal cell with a terminal cell. A single chromoplast can be seen at the bottom of each subterminal cell. This photomicrograph illustrates the unicellular vs multicellular cell character employed in foregoing keys.

Fig. 84 (X 100)

E. angustifolia var. angustifolia race intermedia ray showing pyramidal terminal cells arranged end to end. A series of one and two tiers is shown although three tiers do occur. Overall length of cells having one pyramidal cell range up to 150.0 μ.

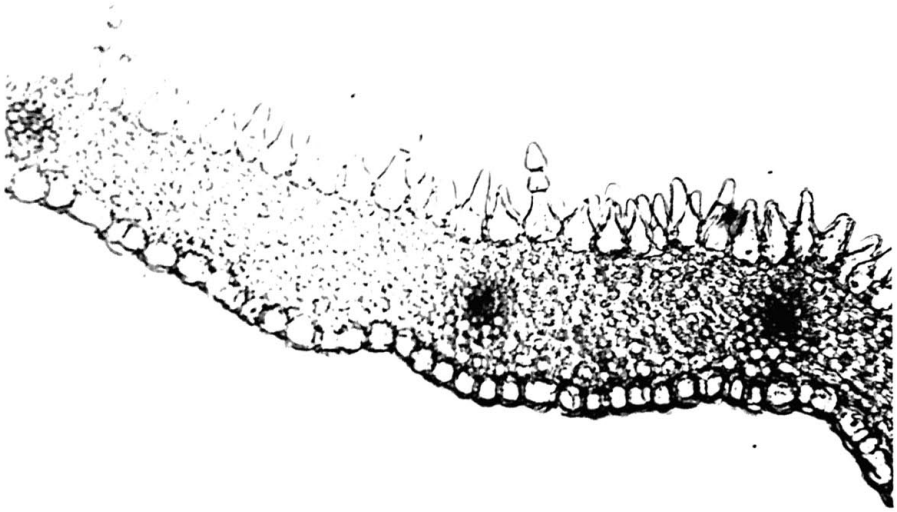
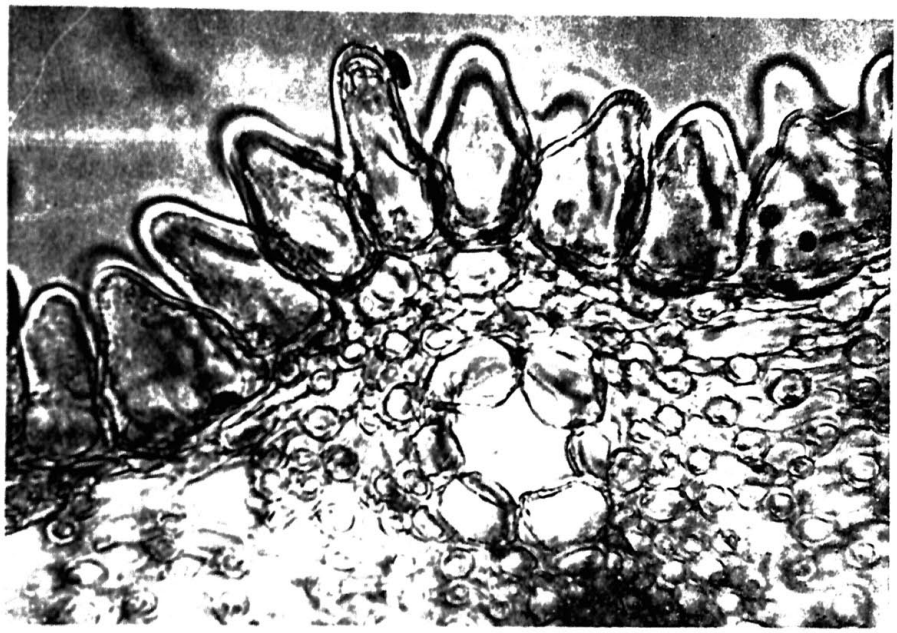


Fig. 85 (X 430)

Transection from E. paradoxa var. neglecta ray showing adaxial epidermal cells and secretory chamber. Notice adaxial position of the secretory chamber unlike many other species. Curiously Fig. 86 has a close resemblance, see text description.

Fig. 86 (X 430)

Shown in transectional view is a ray of E. paradoxa var. paradoxa. Plainly visable in adaxial epidermal cells are chromoplasts. One chromoplastid occurs in each cell. A secretory chamber, ringed with seven epithelial cells, is well-defined.



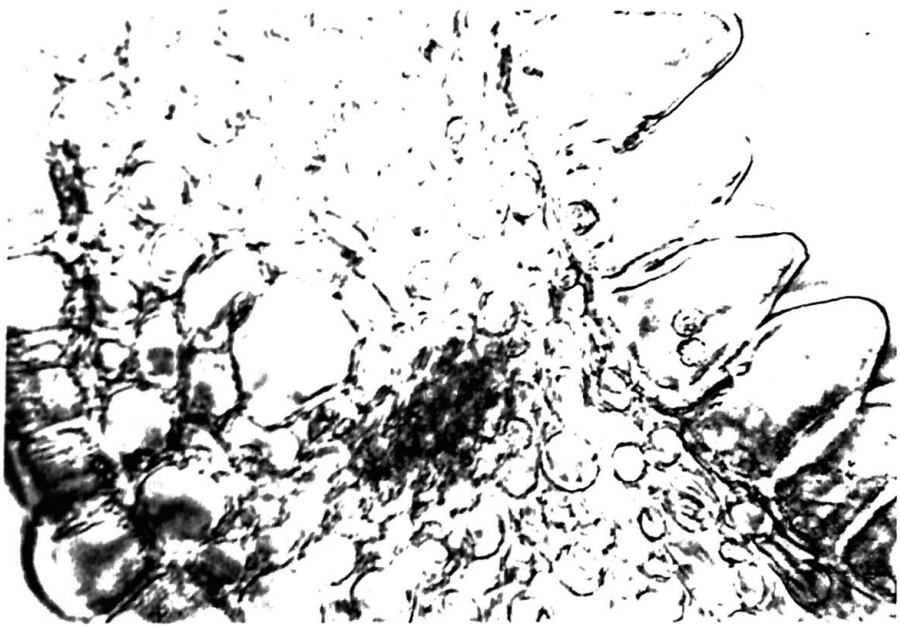
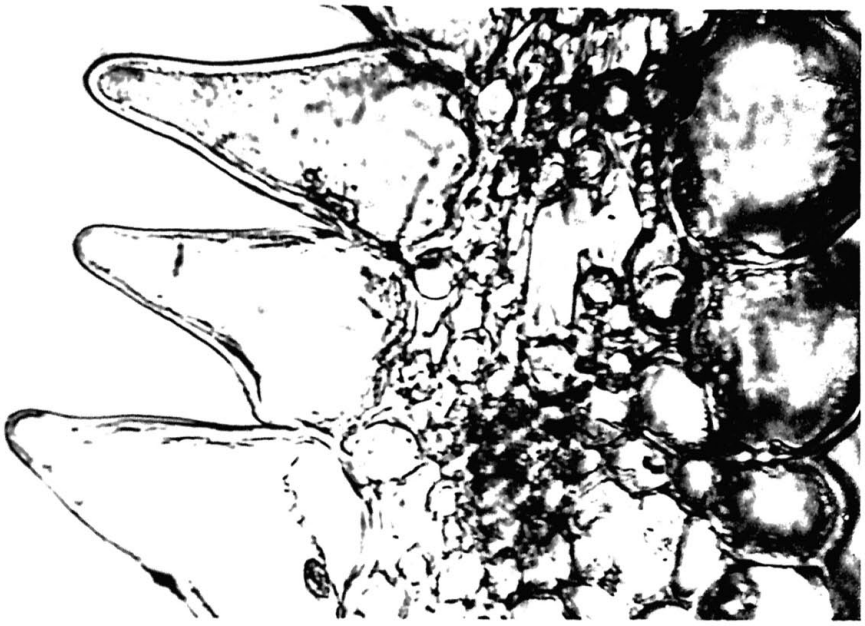


Fig. 87 (X 430)

A portion of Fig. 88 taken under higher magnification. Each ray was prepared by the free hand sectioning method then mounted in glycerol for photographing.

Fig. 88 (X 100)

Shown in sectional view is a ray of E. speciosa. The largest adaxial epidermal cells reported for the genus Echinacea. Note an abaxial epidermis with spherical cells. Surrounding each vascular strand is thick-walled supporting tissue. Noteworthyis the apparent lack of a secretory system.



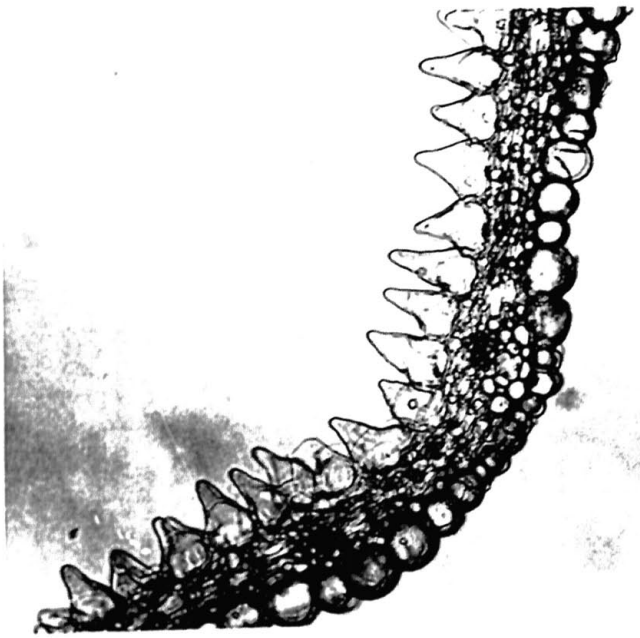


Fig. 89 (X 430)

Shown in trans-sectional view is a ray of E. laevigata. The adaxial epidermal cells appear bullet-shaped. Of special interest is the undifferentiated mesophyll with armed cells.

Fig. 90 (X 430)

Shown in trans-sectional view is a ray of E. pallida. Note the outer tangential wall of adaxial epidermis cells which is modified in varying degrees. Convexity of the outer tangential wall effects shape so important as a diagnostic character.